University of Alberta

Effects of habitat fragmentation on small mammal movement in Banff National Park

by

Wayne Robert McDonald

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of the requirements for the degree of
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in

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled EFFECTS OF HABITAT FRAGMENTATION ON SMALL MAMMAL MOVEMENT IN BANFF NATIONAL PARK submitted by WAYNE R. MC DONALD in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE. in Environmental Biology and Ecology.

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Abstract

Animal movement in fragmented landscapes is typically impeded by barriers that dissect the landscape and enhanced by corridors that facilitate movement across barriers or inhospitable matrix habitat. I translocated three species of microtene rodents (meadow voles [*Microtus pennsylvanicus*], deer mice [*Peromyscus maniculatus*], and red-backed voles [*Clethrionomys gapperi*]) across barriers and corridors to test how animals respond to these landscape elements. Overall, individuals were 20% less successful returning and had more complex paths at artificial compared to natural barriers, suggesting that artificial barriers are somewhat less permeable to movement. Animals returned most successfully across smaller crossing structures and structures with more overhead cover at their entrances than across larger structures or structures with less cover. These results suggest that small mammals may be sensitive to the risk of predation they perceive in corridors lacking concealment. Finally, animals returned less successfully as the distance from crossing structures increased. This response was inversely proportional to home range size among the three species, suggesting that species with larger home ranges can travel farther to use corridors.

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Chapter 1 - General Introduction

Habitat fragmentation has been implicated as a direct cause of declining animal populations around the world (Andreassen et al. 1998, Bowers & Dooley 1999), partly because it can severely disrupt animal movement among remaining habitat patches (Diffendorfer et al.1995, Fahrig 1997). Constraining individual movements among patches can cause populations to become isolated from one another, leading to increased inbreeding and loss of genetic variation at the population level (Burkey 1989, Gerlach & Musolf 2000). These effects are not immediately realized because habitat fragmentation occurs through a continuum from the initial dissection of the landscape by a linear disturbance or barrier through to an attrition stage where suitable habitat patches are imbedded within an inhospitable matrix (Hunter 1996). Even the initial barrier-stage of can affect landscape connectivity by influencing the movement of organisms among patches (Wiens et al. 1985, Forman 1995), influencing animal foraging patterns (Crist et al. 1992), home range use (Loehle 1990, Ims et al. 1992), and dispersal behaviour (Kozakiewicz 1993, Peacock and Smith 1997).

Although much work has been aimed at addressing the effect of fragmentation on movement, the majority of this effort has been concentrated at the attrition stage of fragmentation (Terborgh 1974, Fahrig and Merriam 1985, Temple and Cary 1988, Yahner 1988, Bennett 1990). However, fragmentation is often accompanied by associated habitat loss at the attrition stage, meaning that impacts attributed to fragmentation such as increased isolation of patches may actually be caused by habitat loss (Robinson et al. 1992, Hunter et al. 1995, Fahrig 1997). Some of the potential confounding effects of fragmentation may be separated from those of habitat loss by

concentrating research efforts at the dissection or barrier stage where very little habitat loss has occurred.

A proposed method of improving the ability of animals to move across barriers and unsuitable matrix habitat is to create corridors that connect isolated areas of favoured habitat (often forest; Noss 1987, Bennett 1990, Merriam 1991, Saunders et al. 1991). However some controversy surrounds the role of corridors in species conservation (Noss 1987, Simberloff and Cox 1987, Hobbs 1992, Simberloff et al. 1992, Beier and Noss 1998) because monitoring corridor use can be logistically difficult, particularly when using traditional techniques such as mark-recaptures studies (e.g. Bright 1998, Haddad 1999). To accurately assess corridor efficacy, direct measures of corridor use should be identified, such as the precise trajectories of moving animals while they travel to find and use corridors (Turchin 1991, Tischendorf and Wissel 1997, Haddad 1999).

The ways in which individuals perceive and respond to landscape elements in fragmented habitat, such as barriers and corridors, may be a function, not only of landscape configuration, but also of the activity strategy and habitat requirements of the animal (Ims 1995). A diurnal animal may perceive barriers and corridors differently than nocturnal species due to temporal discrepancies in predation risk and microhabitat conditions. Nocturnal species may experience a lower probability of predation because many predators are not active at night and potential prey may be less detectable in the dark. This reduced detectability at night should result in less dependence on ground cover, which confers greater freedom of movement for nocturnal animals, as they are not constrained by vegetative structure. The perception of barriers and corridors may also depend on the habitat use patterns of animals (generalists vs. specialists). Habitat

generalists do not reside in or rely upon any particular habitat type, whereas specialists almost exclusively use areas dominated by a particular vegetation type or composition (Andren 1992, Garman et al. 1994). As such, generalist species may perceive the habitat discontinuity created by a barrier or corridor as more permeable than a habitat specialist, and correspondingly move more directly across these features.

Documenting the impact of activity and habitat use patterns on movement may be an important component in developing an understanding of animal movement in fragmented landscapes. However, obtaining more reliable knowledge about the effects of fragmentation in the context of species life-history may be best accomplished at the dissection stage in the relative absence of habitat loss (*sensu* Parker & MacNally 2002). Habitat dissection in the last century is well illustrated by the recent proliferation of road networks, with ecological effects extending far beyond the roadway proper (Forman and Alexander 1998). In many areas, road densities are such that the landscape resembles a highly fragmented area, where the effects of one road are confounded by nearby roads and, to some degree, by habitat loss (Bennett 1992, Forman and Alexander 1998). Environmental problems associated with roads are of particular concern in protected areas such as Banff National Park that are crucial in preserving the biodiversity of threatened habitats (Page et al. 1996). In Banff, anthropogenic modification of the surrounding landscape by the Trans-Canada Highway (TCH) creates a potential barrier that influences animal movement within the critical montane habitat of the Bow Valley corridor (Page et al. 1996). In many areas of the Bow Valley, the TCH creates a single linear barrier through otherwise continuous forest habitat, providing an excellent opportunity to study the effect of barriers on movement in continuous habitat. A similar

opportunity exists to study the ways that corridors can mitigate the influence of barriers by examining the highway mitigation passages (overpasses and underpasses) that have been constructed by the Park in an effort to improve the ability of animals to cross the TCH.

A number of studies conducted in Banff have attempted to assess the responses of large animals to the TCH and the associated underpasses and overpasses (e.g. Clevenger & Waltho 2000, Clevenger, Chrusz, & Gunson 2001, Gloyne & Clevenger 2001, Gibeau et al. 2002), some of which focused on large carnivores and ungulates. Rather than using these species which are relatively rare and secretive, a manipulative and replicated approach is possible with small mammals. This study taxa have a number of logistical advantages over large mammals including small home ranges, relative abundance, and ease of capture. Ims and Stenseth (1989) and Matter and Mannan (1989) were among the first to recognize the utility of small-scale manipulations, terming them Experimental Model Systems (EMS). Using EMS, studies conducted at fine spatial scales can potentially be used to predict patterns and processes observed at much broader spatial scales. Manipulating spatial parameters at broad scales is understandably daunting; the costs and difficulties may be prohibitive in all but a few cases. In contrast, spatial patterns can be manipulated at finer scales, perhaps yielding results that can be extrapolated to broader scales.

A number of studies have been conducted that recognized the potential role of small-scale manipulations in ecological investigations. For instance, Crist et al. (1992) examined the role of vegetation heterogeneity in determining the movement patterns of three species of darkling beetles (*Eleodes*) (also see Wiens et al. 1997 for similar

discussion). They found that although differences in movement parameters exist when examined at a particular scale, these behavioural patterns could be extrapolated across a limited range of scales (0.01 to 25 m^2). While Crist et al. (1992) demonstrated that beetle movement parameters were similar when scaled appropriately; they only provided theoretical evidence that movement can be extrapolated across scales. No attempt was made to scale-up to other species occupying broader spatial scales. In contrast, Ims et al. (1992) attempted to use root vole (*Microtus oeconomus*) space use patterns to explicitly predict responses of capercaillie grouse (*Tetrao urogallus*) in fragmented habitats. They found that root voles and capercaillie grouse display similar space use patterns, at fine scales and broad scales respectively, when measured relative to home range size and territorial behaviour (Wiens et al. 1993). This study provided a demonstration of the applications of EMS to extrapolate between different species and across a wide range of spatial scales (0.5 ha to 1000 ha). While the magnitude of the difference in body size and spatial scale that these researchers were able to extrapolate across is somewhat unusual, but the results provided by model systems can often be applied to other systems and spatial scales.

In Chapter 2, I used the movement trajectories of small mammals to measure the permeability of the Trans Canada Highway in Banff National Park to movement relative to natural barriers (forested medians) and continuous habitat (both meadows and forests). In Chapter 3, I determined those elements that promote crossing structure success for small mammals with a focus on the effect of structure type on crossing structure use, the role of cover in crossing frequency, and the distance animals will travel to use a crossing structure. For all of the experiments, mice and voles were translocated across the TCH

from their original capture location to the opposite side of three barrier configurations and coated with fluorescent dye, which later rubbed off as animals moved along the ground, permitting fine-scale monitoring of movement paths. The resulting trails were followed to obtain detailed information on two scale-dependant movement parameters; return success and tortuosity (or complexity) of movement paths, as well as a scale-independent metric of movement, the fractal dimension. By examining the movement patterns of small mammals relative to barriers and corridors with different species of mice and voles, I am attempting to assess how species-specific perceptions affect the responses of animals to these landscape elements.

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Chapter 2 - The effect of artificial and natural barriers on the movement of small mammals in Banff National Park

Introduction

Barriers between adjacent habitat patches are formed early in the continuum that defines the process of habitat fragmentation and occur when linear landscape elements dissect areas of continuous habitat (Hunter 1996). The early stages of fragmentation are associated with very little habitat loss (Robinson et al. 1992), and thus represent a unique opportunity to address fragmentation effects, such as the influence of barriers on animal movement, in the absence of the confounding effects of habitat loss (Stamps et al. 1987, Dunning et al. 1992, Fagan et al. 1999). Barriers can act as effective impediments to animal movement between habitat patches (Kozakiewicz 1993), or can affect their movement by creating more complex movement paths as individuals approach a barrier, withdraw, and approach again. By isolating patches, barriers can reduce visitation and immigration rates, alter patterns of gene flow (Andrén 1994), and affect the persistence of the inherently smaller populations that reside in isolated patches (Wilcox & Murphy 1985).

A variety of empirical studies have demonstrated that barriers can affect animal foraging routes (e.g. Crist et al. 1992), home range use (e.g. Ims et al. 1992), and dispersal behaviour (e.g. Kozakiewicz 1993). However the effect of barriers on animal movement may depend in part on whether the barriers are created naturally or artificially (Crist et al. 1992). Movement patterns may change in association with natural and artificial barriers due to differences in barrier permeability as determined by the physical

characteristics of barriers (Wiens et al. 1985, Forman 1995) and species-specific perceptions of barrier permeability (Zollner & Lima 1997). Species-specific differences in the perception of, and response to, barrier permeability may depend on life-history characteristics (Ims 1995), ranging from body size to activity pattern and habitat selection. Quantifying the degree to which anthropogenic barriers disrupt animal movement between habitat patches also requires comparisons with natural barriers, which exist in all habitats. Additional context is provided by knowledge of animal movement characteristics in relatively continuous habitat.

The potential impact of barriers on animal movement is of particular concern in industrialized nations where roads have proliferated rapidly in the latter half of the 20th century as ubiquitous anthropogenic barriers (Forman 1998). Roads have a number of ecological effects (Trombulak and Frissel 2000), but the most damaging seems to be the disruption they cause to animal movement (Forman 1998), reducing the rate of transfer of individuals between populations divided by barriers and potentially causing genetic differentiation (Aars & Ims 1999). Roads tend to inhibit the movement of small mammals (Kozel & Fleharty 1979), perhaps due to several factors including traffic volume, road surface type, and road width (Oxley et al. 1974). Even relatively narrow and rarely used roads can affect animal movement (Barnett et al. 1978, Burnett 1992), but busy highways ≥ 90 m wide may completely prevent movement (Oxley et al. 1974). Such a severe road barrier appears to exist in Banff National Park where dissection of the surrounding landscape by the Trans-Canada Highway (TCH) clearly interferes with the movement of a variety of large animal species across the Bow River Valley (Clevenger & Waltho 2000). In recent decades, twinning of the TCH (i.e. expanding it from two to four

lanes with a median) has created not only additional artificial barriers, but also natural barriers, or at least ecotones, in the form of grassy and forested medians that divide the highway. The various barrier configurations in Banff provide an opportunity for replicated, manipulative experiments aimed at addressing the characteristics of different types of barriers that may influence animal movement through habitat fragmented by roads.

Basic questions concerning the effect of the physical characteristics of barriers and species-specific perceptions on movement paths have relevance to all animals contending with fragmented habitats. However, they are difficult to address with many of the rare and wide-ranging animals that have been studied in natural landscapes, so I used three species of microtine rodents (meadow voles [*Microtus pennsylvanicus*], deer mice [*Peromyscus maniculatus*], and red-backed voles [*Clethrionomys gapperi*]) for which some responses may be generalized to other species. For these smaller species the barriers created by the highway may not only fragment their habitat, but may also represent some degree of habitat loss. All mice and voles were translocated (*sensu* Crist et al. 1992, With 1994, Zollner and Lima 1999) across different barrier configurations to areas of similar habitat. Using these translocation experiments, I chose to examine how an anthropogenic barrier might affect movements compared to natural barriers, how it influenced path characteristics adjacent to the barrier, and how movement patterns change at different spatial scales.

The responses of mice and voles to barriers may also be affected by differences in natural history characteristics (Ims 1995). This variation includes differences in preferred habitat (open grasslands for meadow voles, forested habitats for red-backed voles, and

either habitat type for deer mice), diel activity patterns (meadow voles are primarily diurnal whereas the other two species are generally nocturnal), and home range size. This variation in addition to their small size, abundance and ease of handling make microtines ideal subjects for experimental manipulations (i.e. using an Experimental Model System approach *sensu* Wiens et al.1993; see also Ims and Stenseth 1989, Matter and Mannan 1989, With et al. 1999) designed to examine basic biological mechanisms.

To extrapolate the principals obtained from small-scale studies conducted with microtine rodents to larger spatial scales, and possibly other species, requires that aspects of scale be equalized across treatments. Fractal analysis (Dicke and Burrough 1988, Wiens 1989, Sugihara and May 1990, Wiens et al. 1995) can be used to allow movement effects to be more easily generalized across spatial scales (e.g. Crist et al. 1992, Ims et al. 1992) by comparing path tortuosity (the degree to which a path twists) with scale-independent metrics. Fractal analysis may or may not represent a scale-independent metric of movement (Turchin 1996), but fractal dimensions have been used successfully to assess movement across a range of spatial scales in a scale-independent manner (With 1994, Nams 1996). This study was designed to measure the permeability of the Trans-Canada Highway to small mammals relative to natural barriers (forested medians) and continuous habitat (both grassy and forested).

Methods

Field data were collected from 1 July to 15 October 1999 and 2000 in the Bow River Valley along the Trans-Canada Highway in Banff National Park, Alberta, Canada. The TCH in Banff extends along the bottom of the Bow valley along with the Bow river, numerous secondary roads, and the Canadian Pacific Railway. The TCH is a major

transportation corridor that carries as many as 5 million people through the park per year (Clevenger & Waltho 2000). Over half of the length of the TCH within the park is four lanes, bordered on both sides by a 2.4 m high wildlife exclusion fence. The remaining portion of the highway is two lanes, however plans exist to upgrade the highway to four lanes and to fence it on either side. Deer mice, meadow voles, and red-backed voles were captured using Longworth live-traps baited with sunflower seeds and individuals were marked for permanent identification using numbered metal ear tags (National Band and Tag Company, Monel™ #1). Captured individuals were then sexed via examination of ano-genital distance, inspected to determine reproductive condition, and weighed with a Pesola spring scale to determine age classes (adult or juvenile).

I conducted translocations to standardize the motivation that individuals would have to cross different barrier configurations in the course of returning to their home territories. This method involved capturing individuals three times to establish their residency and then translocating them to release points at standardized distances. To assess differences in barrier permeability, I translocated all species similar distances across an artificial barrier (the TCH, n = 21), across a natural barrier (the forested median of the TCH, n = 18), and in continuous habitat (in both grassy habitat along the TCH [n = 23] and in forest habitat [n = 22]; Fig.2-1). Prior to their release, all animals were marked with dye by rolling individuals gently in a plastic bag containing a small quantity of fluorescent powder (Radiant™ fluorescent pigment). The dye, which later fell off as animals moved along the ground, permitted fine-scale monitoring of movement paths (Lemen & Freeman 1985, Mikesic & Drickamer 1992).

Movement responses to barriers were quantified as the return success and path characteristics of individuals as they encountered barriers. Traps at the original capture location were monitored for 4 days post-translocation to assess the proportion of translocated animals that successfully returned. Any animal that did not return in this time was captured at or near it's release location and returned manually which allowed me to determine the fate of all translocated individuals. No experimental subjects disappeared or were killed on the highway following translocations (N = 84), therefore every translocated animal was attributable to either success (n = 50) or failure in crossing (n = 34).

All translocations were performed immediately adjacent to the TCH to standardize the effect of traffic volume (i.e. via noise, movement, or vibrations) across barrier types. Mice and voles were released 5 m from the barrier at the beginning of their active periods; early morning for diurnal meadow voles and early evening for nocturnal deer mice and red-backed voles. The subsequent trail of each translocated individual was tracked the next evening at dusk via a hand-held ultraviolet light, which causes the pigment in the dye to fluoresce, revealing a bright trail that represented the animal's precise trajectory. I placed wire pin flags on the trails at each turn where the compass bearing differed by at least 20 degrees from the previous bearing (Turchin 1998). These compass bearings were then converted to turning angles for subsequent analysis by subtracting the compass bearing of each step from the bearing of the subsequent step.

To assess path characteristics such as tortuosity, the turning angles for each path were used to determine the step lengths (the straight-line distance between sequential turns) for all paths. Step lengths and turning angles were then converted into XY

coordinates which allowed me to calculate the squared net displacement of the path, or the square of the total distance that an animal has traveled from the release point to the end of the path in a given habitat. Because measures of simple net displacement will tend to be biased in both duration and length by longer paths (Wiens et al.1993), I employed net displacement squared, which is expected to increase linearly with time (Turchin 1998). Dividing the total path length by the net displacement squared yields an estimate of the overall path tortuosity, which I considered to reflect the energetic costs associated with a particular movement pattern.

To quantify the degree to which barriers disrupt animal movements, I required an estimate of animal movement rates in continuous habitat as a benchmark because translocations performed in the road verge, which would not exist as habitat in the absence of the road, would potentially also result in unnatural movement trajectories. Movement in continuous habitat was documented by conducting translocations of deer mice, red-backed voles, and meadow voles at distances of 80 m and 100 m apart in both closed forest habitat and in the open grassy verge habitat adjacent to the TCH. Translocations in the forest habitat provided an indication of the natural movement characteristics of forest specialist red-backed voles and generalist deer mice, while translocations in the grassy habitat performed a similar function for open habitat specialist meadow voles as well as deer mice. Translocation distances in both continuous treatments corresponded to the range of distances that animals were translocated in the artificial and natural barrier treatments.

Vegetation data for each path determined what, if any, portion of the path was positioned within the barrier versus outside the barrier with particular relevance to the

natural barriers that were defined by the forest-verge ecotone. By separating the path in this manner I determined whether there were observable differences in path tortuosity and fractal dimension when animals encountered the barrier edge (Tischendorf and Wissel 1997, Haddad 1999) versus when they were within the barrier habitat. I considered vegetation structure measured at every third step length and turning angle was of an adequate resolution to determine the location of the barrier edge (after Anonymous 2001). Vegetation measurements included identification of the substrate type (e.g. bare ground, leaf litter, moss, woody debris) and cover type (e.g. grass, shrubs, and coarse woody debris) as well as estimates of cover density (0 to 100% of a 225 cm^2 area in one quarter intervals) and mean cover height in a 225 cm^2 area in the center of every third step length and turning angle.

I analyzed the binary dependant variable, return success, with logistic regression using a model building-strategy described by Hosmer and Lemeshow (1989). Univariate tests to identify significant main effects from all candidate variables were conducted with an alpha level set liberally at 0.25 to allow for the inclusion of biologically important variables in the model. Species type (deer mice, meadow voles, and red-backed voles), translocation type (artificial, natural, and continuous), and sex were identified *a priori* as potential candidate variables. All variables that were significant in the univariate tests were fitted into a combined model, and variables identified as significant using Wald statistics were fit in a reduced model. To assess the effect of variables that were removed, but confounded with the remaining variables, changes in the *beta* coefficients of the remaining variables, with and without the non-significant variables, were examined. The linear assumptions of the continuous variables were tested using a

likelihood ratio test comparing a model containing only the linear term to a model with the addition of the quadratic term. Potentially biologically important interaction terms were entered, one term at a time, into the reduced main-effects model. The significance of these interaction terms was assessed with Wald statistics and verified with a likelihood ratio test examining changes in deviance between the models with and without the interaction term. Finally, a reduced model with the significant main effects and interaction terms was constructed and it's fit to the data assessed using the Nagelkerke's r^2, which provides an approximate measure of the strength of association between the dependent and independent variables. The Hosmer and Lemeshow test statistic was also used to assess the fit of models produced by the logistic regression model (1989). Hosmer and Lemeshow probability values approaching 1.0 indicate that the candidate model fits the data quite well. The qualitative results of the analyses were unchanged with an automated backward stepwise logistic regression procedure.

I used multi-variate ANOVAs to analyze scale-dependant path elements such as tortuosity, fractal dimension, and squared net displacement. Species type (deer mice, meadow voles, and red-backed voles), translocation type (artificial, natural, and continuous), path position (portions of the path inside the barrier and outside the barrier), and sex were identified *a priori* as potential candidate variables. Two-way interaction terms were entered into the model (species by translocation type, species by sex, and sex by translocation type). I used a Tukey's honestly significant difference (HSD) test to determine the significance of pairwise comparisons among several means (Zar 1996). The model's fit to the data was assessed using the adjusted r^2. Tortuosity, net

displacement squared, and fractal dimensions did not meet assumptions of normality, so log transformations were performed to normalize the data.

I used fractal geometry as a scale-independent measure of movement responses. I conducted fractal analysis using the Fractals program (Nams *in press*) that estimates the fractal dimension (D) of a movement path. The logic of the fractal approach can be understood intuitively by considering two extremes of movement; a perfectly straight line where the spatial dimension D = 1 and an infinitely convoluted or twisty path where D = 2. The main assumption of the fractal approach is that the fractal dimension is scale-independent, thus if one measured D for a movement trail at a scale of centimetres long it would be the same as D measured at a scale of meters or kilometres long (Turchin 1996). Scale-independence also implies that if path 1 has a lower overall D than path 2, path 1 is straighter at every spatial scale. There is some debate as to whether fractal D is inherently scale-independent (Wiens et al. 1995) or whether scale independence is an assumption that has to be tested (Turchin 1996), possibly because there are two meanings to the term 'scale-independent.' Scale independence could refer to a property of the estimate. Because D is *estimated* over a range of spatial scales, one measure is yielded over that entire range, and thus the estimator that yields the average value is scale-independent (Nams *in press*). Alternatively, scale independence could refer to a property of the path being measured. If the tortuosity value of the path remains constant across spatial scales, the path itself is regarded as scale-independent (Milne 1988). When an overall D value is estimated for a path, it is assumed that D does not change across the range of scales encompassed by the path. However if D does change with scale the estimated overall D is meaningless.

A simple way to test for scale-independence is to show that log-log plots of path length versus ruler length are linear (i.e. the slope does not change with scale; Sugihara and May 1990). If the log-log plot is linear, the overall estimate of D can be used, but a non-linear log-log plot indicates the presence of more than one domain of scale where, for a given system over a range of scales, the observed fractal D and tortuosity patterns in do not change (Wiens 1989). The presence of domains of scale can be confirmed by calculating the VFractal (Nams 1996). The number of peaks on the VFractal plot of D versus scale yields an accurate estimate of both the number and locations of different domains of scale along a movement path. I used a chi-square test to assess whether the number of domains of scale differed for the three barrier types. A comparison of differences in the scale of the domains along paths was made (following Nams *in press*), using an ANOVA analysis with barrier type, species, and sex as independent variables as well as plausible interaction terms. If the presence of more than one domain of scale was indicated along a particular path, I restricted the ANOVA comparisons of D to the same domains (i.e. Domain 1 for artificial, natural, and continuous barriers). By comparing D within domains in this manner, potential problems stemming from dependence among scales can be avoided.

The path orientation of each mouse and vole was measured at all barrier types to obtain an estimate of how animals perceive, and initially orient, to barriers. I defined orientation as the average path direction over the first 5 m of the path, with 0° set relative to the direction of the nearest point on the barrier relative to the release site (Gillis and Nams 1998). I used circular statistics to estimate the mean angle, the angular deviation, and the 95% confidence limits of the mean for the paths at each barrier type (Zar 1996).

For the continuous translocations, I placed a hypothetical barrier 5 m from the release point perpendicular to the straight-line distance between the original capture location and the release point. V-tests (Zollner and Lima 1997) were performed to determine if mice and voles oriented randomly or significantly more towards their home territory, and Mardia-Watson-Wheeler (MMW) tests were conducted to assess differences between the circular distributions of the three barrier types.

As a final and complementary test of whether animals perceive distinct barrier habitats differently within the same species and between species, I used net displacement squared as a scale-dependent measure of barrier response. Comparisons of net displacement squared were conducted only on those portions of paths that were inside the barrier habitat as determined by the vegetation measurements described above. Because there was no real barrier present in the continuous translocations, this treatment category was not included in these analyses. Individuals with higher net displacement within a particular barrier presumably perceived that habitat to be more permeable to movement than animals that are not able to move as far, particularly when such comparisons are standardized by restricting them to the first 10 m in path length only.

Results

The number of translocated animals that successfully returned to their original capture locations was affected by barrier type (Logistic Regression (LR): $x^2 = 10.4$, df = 3, $P = 0.015$) and species (LR: $x^2 = 8.2$, df = 2, $P = 0.021$), but not sex (LR: $x^2 = 0.79$, df = 1, $P = 0.38$) or distance (LR: $x^2 = 0.13$, df = 1, $P = 0.74$). The overall model (LR: $x^2 = 30.6$, df = 7, $P = 0.001$) provided a reasonable fit to the data (*Nagelkerke* $r^2 = 0.72$, Hosmer & Lemeshow (H&L) test: $x^2 = 4.1$, df = 7, $P = 0.77$, % correctly classified in 0 and 1

categories: 83 and 90 respectively). All species were less successful in crossing artificial barriers than natural barriers, but deer mice had higher return success than the other two species across all barriers (Fig. 2-2). Red-backed voles had the highest return success in the continuous forest treatment and meadow voles returned least often, whereas deer mice exhibited intermediate success. Predictably, this pattern was reversed in the continuous grassy treatment where meadow voles exhibited the highest return success. In both continuous forest and grassy translocations, mice and voles were only 20% more likely to return than they were across artificial barriers, suggestive of a moderate biological effect (Cohen 1988). However deer mice, which were only 4% more likely to return in continuous habitat than across artificial barriers, are by far the least affected. In contrast, meadow voles and red-backed voles were more likely to return in the continuous treatments than across artificial barriers (44% and 31% more likely for meadow voles and red-backed voles respectively).

Using data on individual paths, I compared their tortuosity by ANOVA with the variables translocation type, species, path position (inside vs. outside barrier), and sex as potential main effects. Path tortuosity differed among barrier types (ANOVA: $F_{2,92} = 85.8$, $P < 0.001$, *adjusted* $r^2 = 0.73$, Fig. 2-3a and 2-3b). Consistent with the observed pattern for return success, individuals exhibited less tortuous movement paths in the continuous translocations than they did at either the artificial (Tukey's HSD: mean diff = -1.45, $P < 0.001$) or natural barriers (Tukey's HSD: mean diff = -1.31, $P < 0.001$). Unlike return success, however, there was no difference in tortuosity between artificial and natural barriers (Tukey's HSD: mean diff = 0.14, $P = 0.52$). There were also significant differences in tortuosity among species (ANOVA: $F_{2,92} = 3.7$, $P = 0.030$). Meadow

voles, which are primarily diurnal, moved in a significantly more tortuous manner when encountering all barriers than did deer mice (Tukey's HSD: mean diff = 0.32, $P = 0.027$), however no differences in tortuosity were evident between meadow voles and red-backed voles (Tukey's HSD: mean diff = -0.086, $P = 0.78$) or between deer mice and red-backed voles (Tukey's HSD: mean diff = 0.23, $P = 0.19$). There was also a significant effect of path position on tortuosity (ANOVA: $F_{1,92} = 7.3$, $P = 0.09$). Contrary to prediction, animal movement paths were more tortuous when they encountered barriers (mean tortuosity ± standard deviation: 0.012 ± 0.026) than when they were moving within the barrier habitat (mean = 0.0063 ± 0.026 SD). Moreover, meadow voles exhibited much more tortuous paths within natural (forested) barriers than when encountering natural barrier edges, perhaps reflecting the difficulty this species had in moving through this habitat. There were no differences in the tortuosity of paths as a function of sex (ANOVA: $F_{1,92} = 0.16$, $P = 0.69$). A significant interaction between translocation type and species in the degree of tortuosity exhibited for each path revealed that meadow voles showed disproportionately higher tortuosity at artificial and natural barriers which were comprised of habitat other than their preferred open grassy habitat, relative to continuous translocations, while deer mice showed disproportionately low tortuosity at natural barriers (ANOVA: $F_{4,92} = 16.5$, $P < 0.001$). There were no significant interactions between sex and translocation type (ANOVA: $F_{2,92} = 1.34$, $P = 0.27$) or species and sex (ANOVA: $F_{2,92} = 1.06$, $P = 0.35$).

If the presence of more than one domain of scale was indicated along a particular path, I restricted the ANOVA comparisons of the scale-independent fractal dimensions to the same domains (i.e. Domain 1 for artificial, natural, and continuous barriers). Fractal

dimensions of individual paths differed significantly among artificial, natural, and continuous barriers (ANOVA: $F_{2,92} = 335$, $P < 0.001$, *adjusted* $r^2 = 0.93$, Fig. 2-4a and 2-4b). As with the scale-dependent tortuosity measurement, mice and voles had significantly lower fractal values, indicating that they moved in straighter lines with corresponding higher return success, in the continuous treatment than at artificial (Tukey's HSD: mean diff = 0.22, $P < 0.001$) or natural barriers (Tukey's HSD: mean diff = 0.092, $P < 0.001$). Also like the pattern observed for path tortuosity, individuals encountering artificial barriers had similar fractal dimensions to animals at natural barriers (Tukey's HSD: mean diff = -0.0012, $P = 0.091$) and these differences were consistent among species and path locations. Although the qualitative response to different barrier types was similar among species, absolute fractal dimensions differed (ANOVA: $F_{2,92} = 179$, $P < 0.001$). Deer mice paths had lower fractal D estimates than either red-backed voles (Tukey's HSD: mean diff = 0.062, $P < 0.001$) or meadow voles (Tukey's HSD: mean diff = 0.16, $P < 0.001$), and red-backed vole paths in turn had lower fractal values than meadow voles (Tukey's HSD: mean diff = 0.096, $P < 0.001$). Measured by the complexity of their paths, individuals moved less directly outside barriers (mean fractal D ± standard deviation: 1.17 ± 0.123) than inside the barrier habitat (1.14 ± 0.136) (ANOVA: $F_{1,92} = 9.04$, $P = 0.04$). Sex had no effect on the fractal values of translocated animals (ANOVA: $F_{1,92} = 1.91$, $P = 0.17$). Among the three interaction terms I investigated, only translocation type by species was significant, and indicated proportionately more complex paths displayed by meadow voles at artificial barriers (ANOVA: $F_{4,92} = 32.5$, $P < 0.001$) where none of them succeeded in returning.

The number of peaks on a VFractal plot of D versus scale yields an estimate of the number of domains of scale along a movement path, and the positions of peaks on this plot indicates their spatial scales (Fig. 2-5, Nams 1996). Meadow voles interacted with more domains of scale than expected regardless of barrier type, while natural barrier habitat displayed more domains than artificial or continuous barriers (chi-squared test: $x^2 = 13.3$, df = 2, $P = 0.001$). This indicates that meadow voles used vegetation at a larger number of scales than deer mice or red-backed voles (for instance within a single bush, between bushes, and between patches of bushes), while natural (forested) barriers contained more complex vegetative structure than the other barrier types. Sex did not significantly influence the number of domains of scale in movement paths. To assess differences in the positions (i.e. scales) of domains, I used an ANOVA, comparing barrier types, species, sex and their plausible interaction terms. The positions of domains (representing their scales) differed depending on barrier type (ANOVA: $F_{2,62} = 18.3$, $P < 0.001$, *adjusted* $r^2 = 0.38$). Posthoc tests showed that animals translocated in the continuous treatment moved at significantly larger spatial scales in the earliest path domain than animals at either natural (Tukey's HSD: mean diff = 23.3, $P = 0.004$) or artificial (Tukey's HSD: mean diff = 39.6, $P < 0.001$) barriers, probably as a function of a relatively homogenous vegetative structure for animals in the continuous (i.e. grassy) treatment. Interestingly, there was no difference in the scale of movement between natural and artificial barriers (Tukey's HSD: mean diff = 16.3, $P = 0.067$), even though the barriers are composed of substantially different habitats (forest vs. pavement). The three species exhibited significantly different scales of domains along paths (ANOVA: $F_{2,92} = 4.98$, $P = 0.011$). Deer mice movement in the spatial scale associated with the

earliest path domain occurred at a significantly larger scale than meadow vole movement patterns (Tukey's HSD: mean diff = 20.02, $P = 0.010$), meaning that deer mice at the earliest path domain (e.g. within a bush) are able to move further than the other species. Males and females occupied similar scales in the first domain and there were no significant interactions among barrier type, species, or sex. As in the first domain, the scale of domains at the second domain was different at different barriers (ANOVA: $F_{2,62} = 4.64$, $P = 0.017$, *adjusted* $r^2 = 0.22$). At the second domain, animals once again moved at significantly larger spatial scales in the continuous treatment than at either natural (Tukey's HSD: mean diff = 105, $P = 0.015$) or artificial (Tukey's HSD: mean diff = 96.3, $P = 0.024$) barriers, while no difference was evident between natural and artificial barriers (Tukey's HSD: mean diff = -8.6, $P = 0.94$). Species type and sex had no impact on the scale of movement in the second domain, and there were no interactions between any of the main effects. An ANOVA indicated that there were no significant predictors of scale for the third, and final path domain (ANOVA: $F_{4,12} = 0.71$, $P = 0.61$, *adjusted* $r^2 = 0.10$).

As one measure of the way small mammals perceived and responded to barriers in Banff, I measured the initial orientation of translocation paths to assess the perception of barrier edges. Orientation estimates were based on the mean angle of orientation to the original capture location within the first 5m of the path. Mice and voles oriented furthest away from artificial barriers (mean ± 95% confidence intervals = 86° ± 55°; V test: $\mu_{0.05,21} = 0.17$, $P > 0.25$), suggesting that they were perceived to be more of a barrier to movement. For animals released at natural barriers, mean orientation was slightly, but not significantly, more in the direction of the barrier (mean ± 95% confidence intervals =

57° ± 66°; V test: $\mu_{0.05, 18} = 1.29$, $P > 0.10$). By contrast, animals released in the continuous treatment oriented significantly towards the hypothetical barriers' location (mean ± 95% confidence intervals = 20° ± 13°; V test: $\mu_{0.05, 23} = 6.16$, $P < 0.0005$). These results suggest that animals perceived and began to avoid barriers, particularly artificial ones, shortly after their release. I investigated the possibility of species and sex effects on the orientation of mice and voles at barriers using Mardia-Watson-Wheeler (MWW) pairwise tests. There were no significant differences in orientation between sexes (MWW test: $x^2_{0.05, 2} = 5.99$, $0.975 < P < 0.990$) or among species (MWW test: $x^2_{0.05, 4} = 9.49$, $0.05 < P < 0.10$) at the artificial barrier. Animals released at natural barriers also exhibited no significant differences in orientation between sexes (MWW test: $x^2_{0.05, 2} = 3.0$, $0.10 < P < 0.25$). However, among species, deer mice were slightly more likely to orient toward the barrier than red-backed voles and meadow voles (MWW test: $x^2_{0.05, 4} = 8.5$, $0.05 < P < 0.10$). No significant differences in orientation between sexes were observed in the continuous translocations (MWW test: $x^2_{0.05, 2} = 1.93$, $0.25 < P < 0.50$), but there were significant differences among species driven once again by high deer mouse orientation towards the hypothetical barrier (MWW test: $x^2_{0.05, 4} = 10.8$, $0.025 < P < 0.05$).

As a final measure of movement efficiency, I used net displacement squared to show how animals perceive the habitat within different barriers as opposed to barrier edges, expecting that animals would travel farther (i.e. higher values) in habitat that is more permeable. Within the first 10 m of their paths, animals moved 5.7 times farther in natural barrier habitat than on the road surface representing artificial barriers (ANOVA: $F_{1,18} = 44.6$, $P < 0.001$, *adjusted* $r^2 = 0.86$, Fig. 2-6). Deer mice were able to move

significantly further through both barrier types than meadow voles (Tukey's HSD: mean diff = 0.095, $P < 0.001$) or red-backed voles (Tukey's HSD: mean diff = 0.45, $P = 0.023$), while red-backed voles had significantly larger displacement values than meadow voles (Tukey's HSD: mean diff = 0.46, $P = 0.013$; ANOVA: $F_{2,18} = 29.2$, $P < 0.001$). Males and females displaced similar distances in all barrier habitats (ANOVA: $F_{1, 30} = 0.89$, $P = 0.36$). There were no significant interactions among translocation type, species and sex.

Discussion

One goal of this study was to measure the proportion of translocated deer mice, meadow voles, and red-backed voles that successfully crossed artificial and natural barriers, one of the simplest quantitative metrics of barrier permeability (Stamps et al. 1987). Deer mice returned more successfully across the barriers than meadow voles or red-backed voles and this appeared to be due partly to the physical attributes of the barriers themselves. Artificial barriers contain mainly anthropogenic material in comparison with mainly natural vegetation growth in the highway median and verge that more closely resembles the preferred habitat of these species.

Despite the fact that barriers lessened returned success, the reduction was unexpectedly slight given that very narrow roads and even overgrown and long-unused tracks have been shown to eliminate the movement of small mammals (Oxley et al. 1974, Burnett et al. 1978). The movement rates of mice and voles in the continuous forest and grassy treatments, which provide context for their movement across barriers, showed that individuals were only 20% less likely to return across artificial barriers than in the two continuous translocations, indicating that the road is not as much of a barrier to these species as one might expect. Animals should be more comfortable moving through

grassy habitat or forest than across a paved highway devoid of vegetation and full of noisy and dangerous vehicles (Jefferies & Lawton 1984, Kotler & Brown 1988).

Despite this overall conclusion that artificial barriers present only a moderate barrier to movement, the slightness of this effect was caused mainly by deer mice, which almost always returned across artificial barriers, natural barriers and through continuous habitat. This nocturnal generalist may perceive less of a discontinuity between the pavement and the adjacent verge habitat, and experience a lower probability of predation because potential prey should be less detectable at night (eg. Marinelli and Neal 1995). In contrast, meadow voles and red-backed voles were more likely to return in the continuous treatments than across artificial barriers. The differences in the responses of voles and deer mice can probably be attributed to some extent to differences in mobility, which can influence the perception landscape patchiness (Carpenter 1987). Consistent with the fact that both vole species are less mobile than deer mice (Banfield 1981), the road seemed to represent much more of barrier to movement for the meadow and red-backed voles. Red-backed voles responded approximately as predicted based on the expected permeability of the barriers, showing increased success in continuous relative to natural and natural relative to artificial barriers. But it was surprising that meadow voles, which use open grassy habitat almost exclusively, found crossing a patch of woods more difficult than crossing a busy highway, implying that species specific habitat preferences may play an important role in dictating animal responses to barriers (Burnett 1992). Therefore crossing success, the simplest metric of barrier permeability, suggest that a busy highway is only a moderate barrier to movement (after Cohen 1988) for these animals.

Although my results suggest that artificial features, such as roads, present partial barriers to animal movement, it is possible that the barrier effect I measured also reflected differences in navigational abilities. Animals that were captured and released within their home-ranges (plausible for both continuous treatments) would presumably be more successful returning because they were in the presence of familiar cues. This navigational effect may have produced slightly elevated return success in the continuous treatments, relative to those containing barriers. Because small mammals tend to align their territories to physical features such as roads, which results in the organization of social spacing along such features (Barnett et al. 1978, Stamps et al. 1987), it is unlikely that translocated small mammals were released in familiar territory (i.e. their home-range) at natural or artificial barriers (Burnett 1992). Although this navigational effect may have slightly increased return success in the continuous treatment, it cannot explain why animals generally had lower success crossing artificial, than natural, barriers.

Path tortuosity and fractal dimensions were measured to examine the mechanisms potentially responsible for differences in mice and vole return success, as more complex, energetically expensive paths could result in lower return success across barriers (Stamps 1987). Animals generally moved in a more tortuous manner when they encountered artificial barriers, which corresponded to substantially lower return success. Deer mice presumably exhibited much less tortuous paths than meadow voles or red-backed voles because they are a relatively mobile species that are able to use a wide variety of habitats, perhaps making the road appear to be less of a contrast in habitat (Burnett 1992). Meadow voles had disproportionately more tortuous paths at artificial barriers than any other species at any other barrier type, possibly due to their diurnal activity and the

corresponding high traffic volumes along the TCH. During the daylight hours, traffic volumes on the TCH are significantly higher than those occurring at night, varying from peak values of 20 000 vehicles during the day to less than 5000 vehicles at night (Clevenger & Waltho 2000). Consequently, meadow voles encountered elevated vehicle noise, vibration, and movement during their active periods. Higher traffic volumes may have caused meadow voles movements to become more complex as they approached the barrier, assessed the habitat on the other side of the barrier edge, and withdrew when they determined that the adjacent habitat was unsuitable, leading to reduced crossing success.

Movement paths were separated into sections outside versus inside the barriers with vegetation data collected along each path to determine if differences in path complexity at natural and artificial barriers were a result of encountering the edge of the barrier or moving within the barrier habitat. Perhaps the best evidence that barriers generally alter movement comes from individual responses at barrier edges (Buechner 1987), while movement changes within barriers are more of a response to different habitat elements than to a barrier effect *per se*. Movement paths were more tortuous when animals encountered barriers than when they were moving within the barrier habitat, which might indicate that the perceived permeability of barrier edges is the process underlying the observed pattern of return success. Both inside and outside barriers, animals at artificial barriers had higher tortuosity values, but meadow voles exhibited more tortuous paths than the other species. If high tortuosity values inside barriers are caused by vegetative complexity, then natural barriers, which contain shrubs, trees, and grasses in a variety of spatial configurations, should produce the most complicated paths. However this study revealed that the highest tortuosity values occurred inside artificial barriers, which is

somewhat surprising as there is no vegetation on the road surface. Instead, the lack of cover inside artificial barriers may have produced high path complexity because individuals were attempting to elude traffic and potential predators in what they likely perceived as a very hostile environment.

Fractal analysis can be used to allow movement effects caused by barriers to be more easily generalized across spatial scales (e.g. Crist et al. 1992, Ims et al. 1992) by comparing path tortuosity with scale-independent metrics. Because path tortuosity is a scale-dependent metric, any differences observed in path tortuosity that were attributed to species and barrier type may in fact be due to life history differences such as territory size. Species with larger territories such as deer mice (approx. 1.2 ha) may operate on a spatial scale larger than species with smaller territories such as red-backed voles (approx. 0.7 ha) and meadow voles (approx. 0.1 ha; Banfield 1981). Consequently, a scale-independent measure of movement, fractal dimension, was used to discern whether the different movement patterns that were observed were due to the type of barrier or species, or to the fact that deer mice occupy larger home ranges than the other two species. When controlled for scale, animals at artificial barriers generally interacted with the landscape in a more complex manner, while meadow voles had much more complex movement paths than did deer mice or red-backed voles across all barrier types. These results are qualitatively consistent with the tortuosity and return success values described above. Thus, it appears that the movement responses of deer mice, meadow voles, and red-backed voles to barrier permeability are not influenced by spatial scale, or at least by the range of scales encompassed by the territory sizes of these species. This congruence gives me confidence that I have not incorrectly identify one attribute as the underlying

force determining movement patterns and processes (e.g. species life-history) when an entirely different attribute actually drives the observed patterns (e.g. spatial scale).

By assessing the scales at which landscapes elements influence movement, the fractal approach can also be used to identify domains of scale (With 1994), where, for a given system over a range of spatial scales, the observed patterns do not change (Wiens 1989). Identifying domains of scale also allowed all comparisons of D to occur within the same domain, avoiding potential problems stemming from dependence among scales. Meadow voles exhibited more complex movement paths, presumably leading them to interact with more domains of scale regardless of barrier type. Thus, it is plausible to suggest that meadow voles were forced to interact with cover at small scales, for instance within a single bush, at slightly larger scales such as between individual bushes, and at the scale of the entire translocation path (*sensu* Nams *in press*). Similarly, natural barrier habitat contained more domains than artificial or continuous barriers due to more complicated spatial configurations of shrubs, trees, and grasses, although this did not necessarily translate into more tortuous movement paths at natural barriers as one might expect. Therefore while it is important to identify domains of scale along paths so that comparisons of D can be made within the same domain, eliminating potential problems stemming from dependence among scales, the absolute number of domains is not necessarily an accurate reflection of movement responses to barriers. Domains of scale at artificial barriers occurred earliest (i.e. at the smallest spatial scale) presumably because artificial barriers have inherently low permeability with little or no cover along the Trans-Canada Highway, causing animals to alter their movement patterns appropriately by reacting immediately to barrier edges.

Animal responses to barrier edges can be quantified with fractal dimensions, however measurements of individual perception within barrier habitat requires an additional metric, net displacement over a given length of path (10m), to address functional heterogeneity (With 1994). Mice and voles inside artificial barriers did not move as far as individuals in natural or continuous habitat, suggesting that artificial barriers were less permeable to movement. Deer mice, a more robust species, moved much farther than meadow voles or red-backed voles within all barrier types. Various species of mice have been found to perceive their surroundings mainly by sight (Zollner and Lima 1997), while the little direct evidence that exists suggests that voles may use auditory and olfactory cues rather than visual cues to detect landscape elements (Gillis & Nams 1998). Because all translocations were performed adjacent to a busy highway, the sounds and smells associated with traffic may have interfered with the homing cues that animals used to return to their home territory. Therefore, it is not surprising that both vole species were less successful at homing than were deer mice, which probably experienced lower traffic volumes. The negative influence of traffic on the ability of voles to return across the highway may have been mitigated by the fact that some mammal species living adjacent to roads become habituated to the presence of traffic (Sprock et al. 1967). However, all of the translocated individuals were released within 2 m of the barriers and continued to move within 5 m of barriers. Thus, voles moving immediately adjacent to the roads may have experienced a much greater impact of traffic on their ability to navigate by sounds and smells than they normally experienced while moving within their home-ranges.

The orientation of mice and voles relative to landscape elements was used as a second measure of the perceptual abilities of animals (Zollner and Lima 1997, Zollner and Lima 1999). However this orientation metric related directly to the perception of the barrier edge rather than how animals perceived the barrier habitat itself which the net displacement results addressed. No orientation toward the barrier was evident at the artificial barriers perhaps because animals perceived the barrier edge to be relatively impermeable. It is presumably this perception of artificial barrier edges that causes animals to reverse their movement trajectories more frequently, creating more complex, energetically expensive movement patterns (Stamps et al. 1987). The orientation results suggested that animals perceived and began to avoid barriers, particularly artificial ones, shortly after their release. This rapid perception and response to barrier edges is perhaps the behaviour underlying the higher tortuosity values of animals encountering artificial barrier edges rather than the responses of animals moving within the barrier habitat.

In summary, individuals crossing artificial barriers had moderately lower return success and more complex path structures than individuals crossing natural barriers, indicating that artificial barriers are somewhat less permeable to movement. Previous studies have suggested that the proportion of individuals that cross a barrier (Stamps et al. 1987) and the similarity of the matrix to the home habitat (Lidicker 1999) are both factors that determine barrier permeability. My results suggest that the method of barrier creation (artificial or natural) is also important in determining barrier permeability, although pronounced differences occur among species.

Two of my results caution against generality in interpreting road effects. First, the modest effect size of roads on small mammal movement I found, suggests that the TCH

acts only as a filter rather than an absolute barrier as roads do in other locations (Bennett 1992, Forman 1995). The slightness of this effect contrasts with other studies in which even very narrow and rarely used roads restricted animal movement (Burnett et al. 1978, Oxley et al. 1974), or major roads created a barrier sufficient to cause genetic differentiation (Gerlach & Musolf 2000).

A second finding also reduces general interpretations. This study revealed that movement paths were more complicated inside artificial barriers rather than inside natural barriers. Previous studies have shown increased tortuosity to occur in higher quality habitat where more foraging opportunities exist (With 1994, Stapp & Van Horne 1997). Thus, I might have expected that animals inside the natural barrier, which was full of shrubs and trees, would have shown higher tortuosity values reflecting this heightened vegetative complexity. Instead, it may be that higher tortuosity values occurred on the road because of the need to rapidly evade moving traffic, similar to the higher tortuosity that occurs in response to predators (e.g. Kotler & Brown 1988). The various ways in which tortuosity is interpreted belies the generality that might be assumed of this measure in barrier or other contexts.

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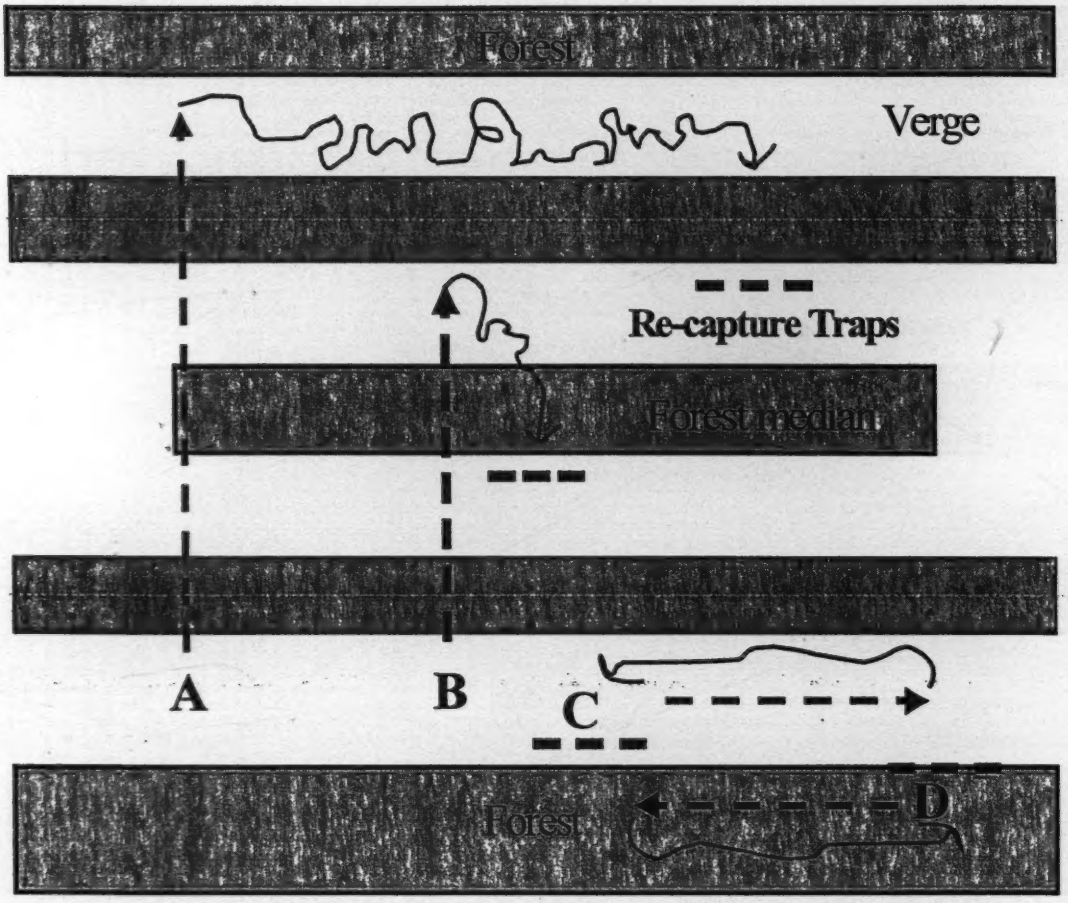

Figure 2-1: Schematic of artificial (2 lanes of the TCH; **A**), natural (forested median of similar width to 2 lanes of the TCH; **B**), grassy continuous (**C**), and forested continuous (**D**) translocations showing original capture, release, and re-capture locations along the Trans-Canada Highway.

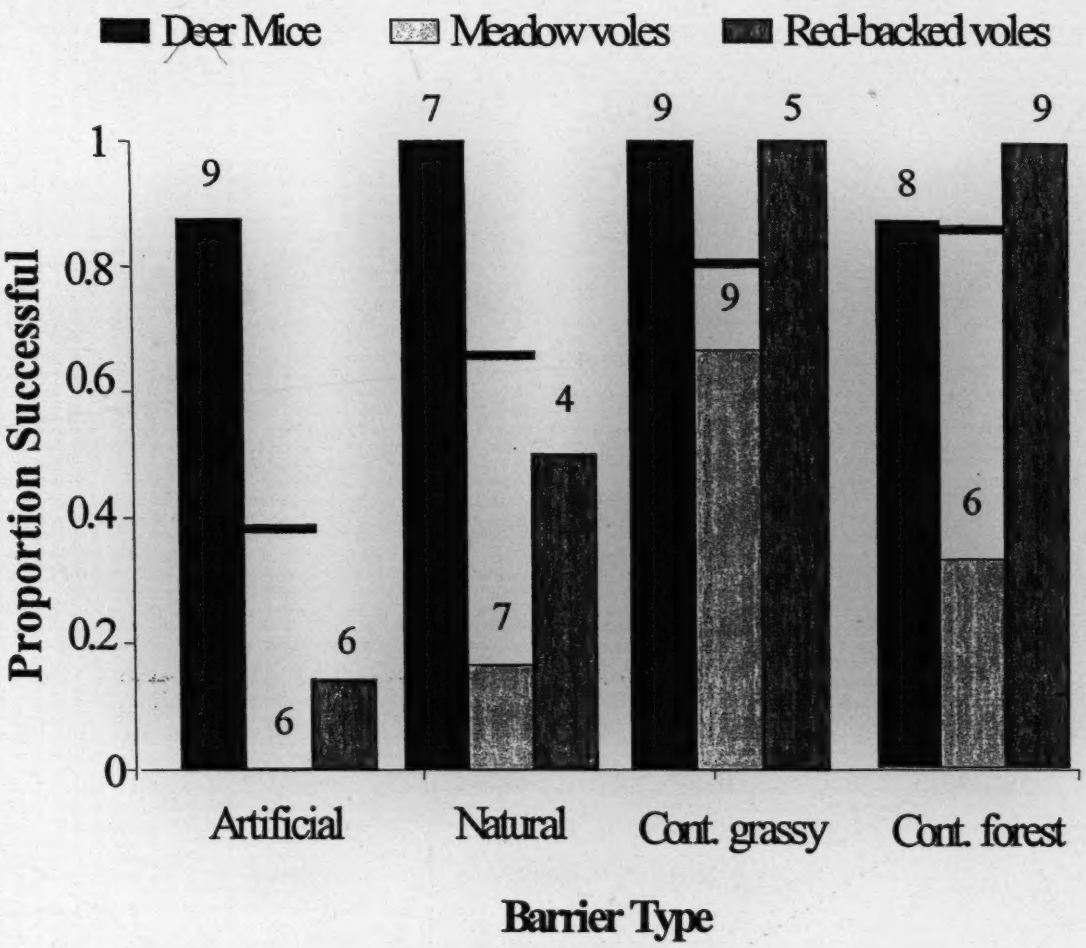

Figure 2-2: Proportion of deer mice, meadow voles, and red-backed voles that successfully returned to their original capture locations following artificial, natural, and continuous translocations. Black lines represent the adjusted means for each barrier type. Sample sizes (n) are above each bar.

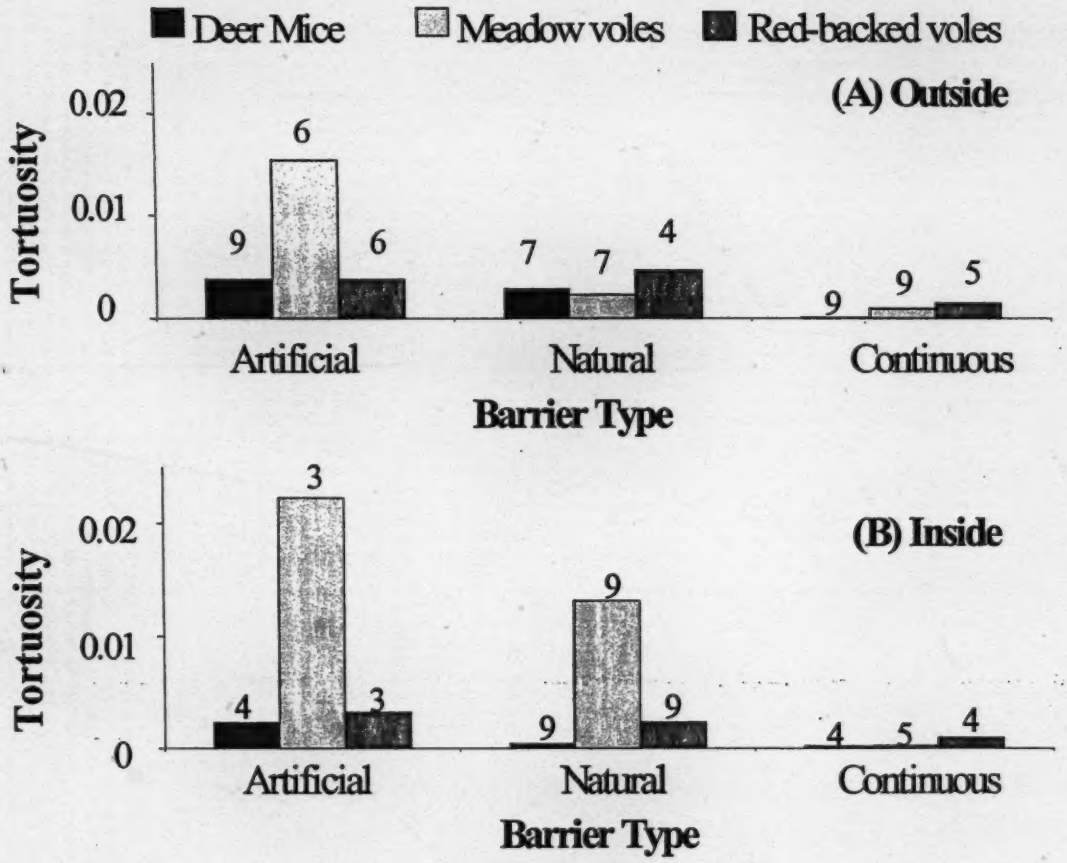

Figure 2-3: Tortuosity values (total path length divided by net displacement squared) of translocated deer mice, meadow voles, and red-backed voles encountering artificial, natural, and no barriers (a) outside and (b) inside barriers. Sample sizes (n) are above each bar.

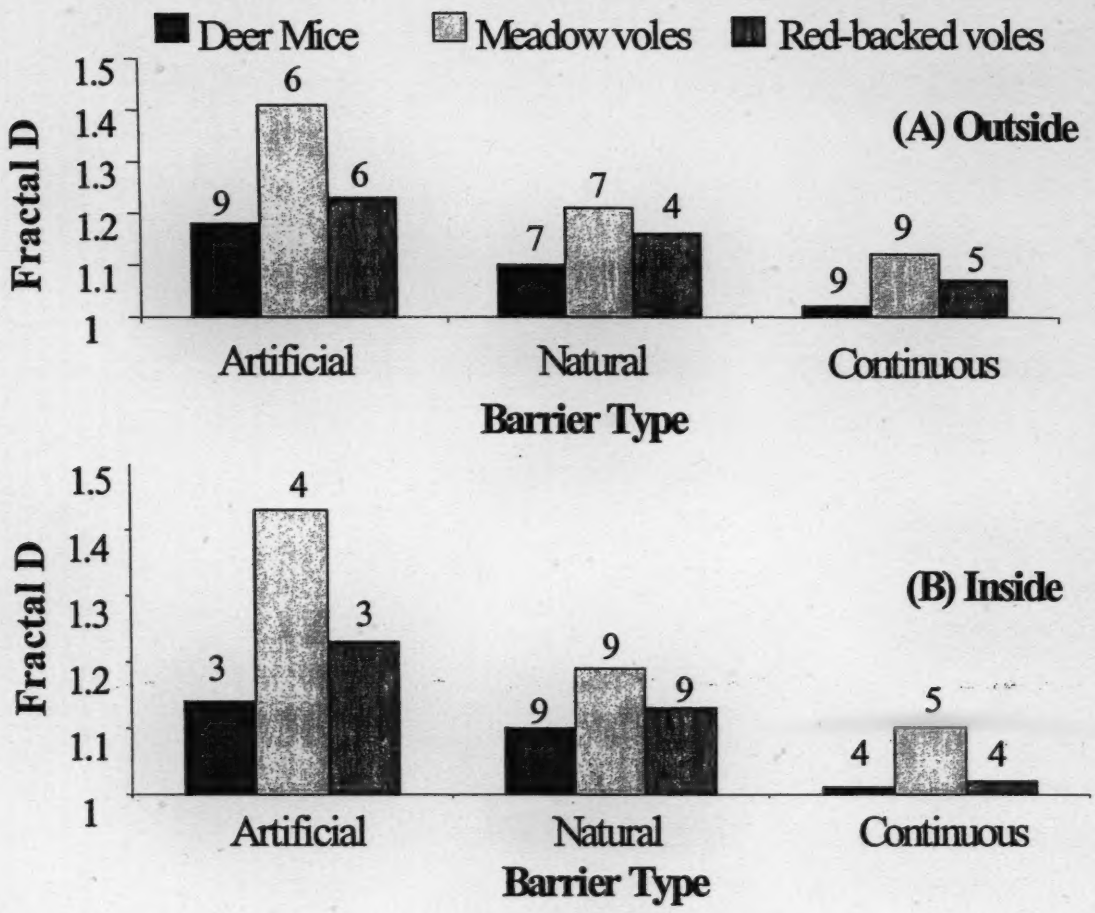

Figure 2-4: Fractal dimensions calculated from the paths of translocated deer mice, meadow voles, and red-backed voles encountering artificial, natural, no barriers (a) outside and (b) inside barriers. Sample sizes (n) are above each bar.

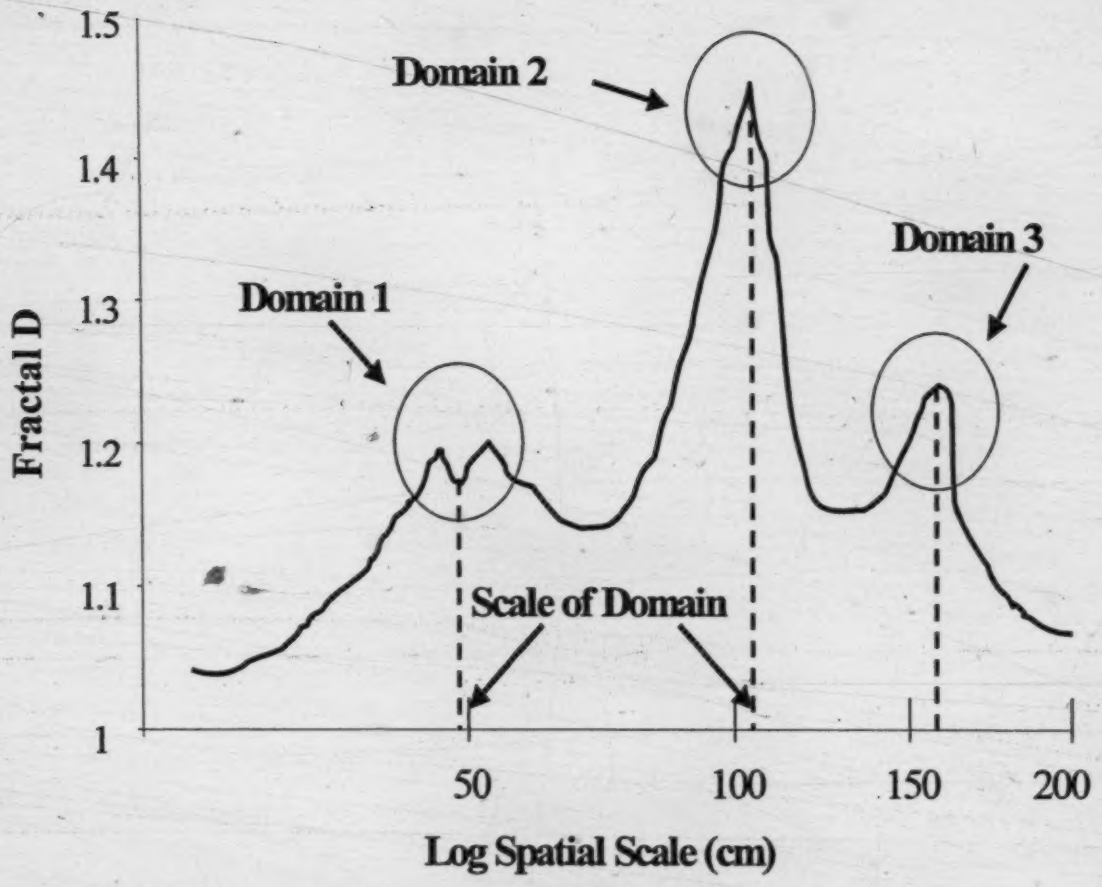

Figure 2-5: Plot of Fractal D versus the log of spatial scale for a red-backed vole encountering a natural barrier. The peaks in the line represent Domains of scale where observed patterns do not change. The spatial scale of each Domain can be estimated by extrapolating a line from the middle the peaks directly to a point on the X axis.

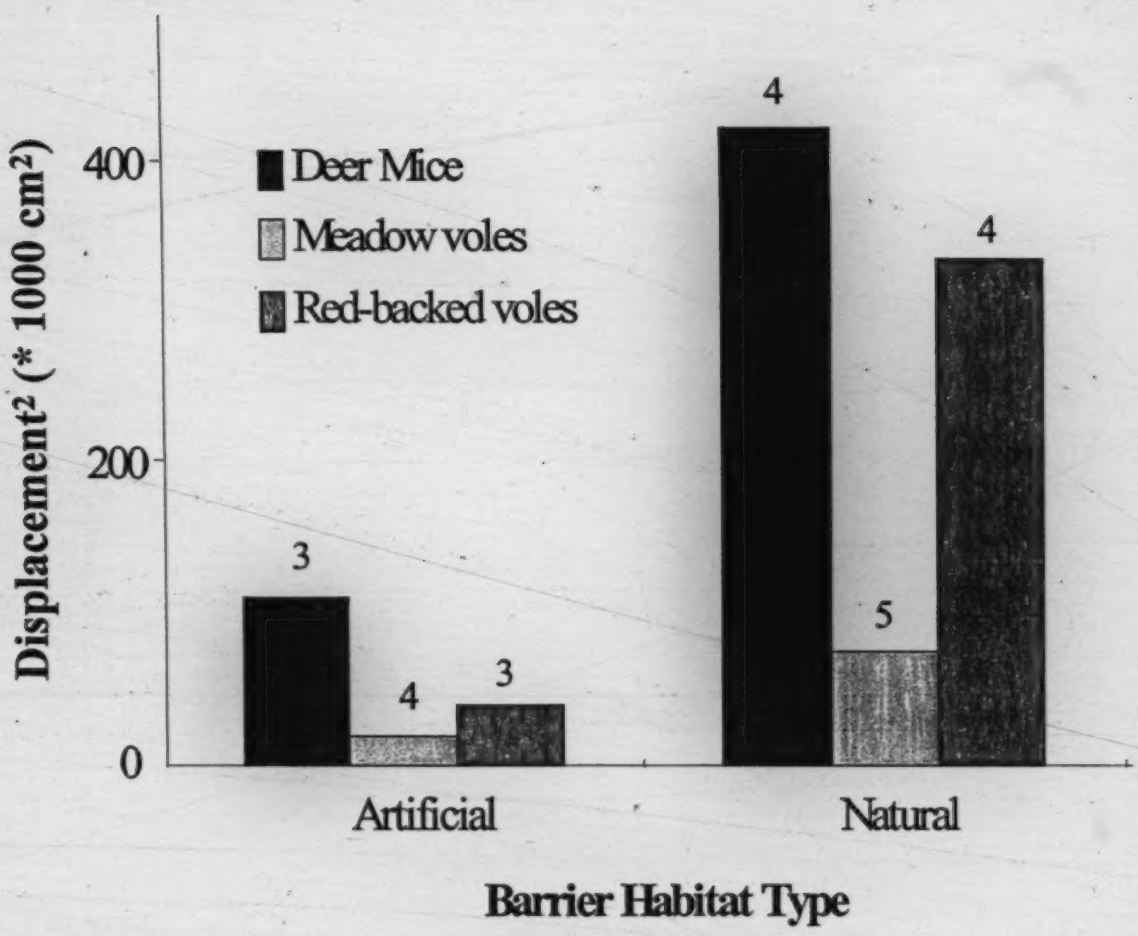

Figure 2-6: The displacement distances (defined as the straight line distance between the beginning and end of movement trails and measured for the first 10m of the paths) for translocated deer mice, meadow voles, and red-backed voles moving through artificial and natural habitat. Sample sizes (n) are above each bar.

Chapter 3 - Determining the elements that promote crossing structure success for small mammals in Banff National Park

Introduction

Corridors have been widely advocated as essential components of reserve design because they can connect isolated areas of suitable habitat and thus minimize the harmful effects of habitat fragmentation on animal movement (Noss 1987, Bennett 1990, Merriam 1991, Saunders et al. 1991). A lack of movement in fragmented landscapes can reduce visitation and immigration rates, alter patterns of gene flow (Andrén 1994), and affect the persistence of the inherently smaller populations that reside in these isolated patches (Wilcox & Murphy 1985, Fahrig and Merriam 1994, Rosenberg et al. 1997). Despite the intuitive logic of corridors, there remain unanswered questions about whether corridors actually facilitate animal movement among remaining habitat patches (Noss 1987, Simberloff and Cox 1987, Hobbs 1992, Simberloff et al. 1992, Beier and Noss 1998), mainly due to a lack of empirical evidence (Rosenberg 1997).

Much of the support for the role of corridors in species conservation is theoretical, however recently there has been empirical evidence from microcosm studies that demonstrate increased population persistence in the presence of corridors (Gilbert et al. 1998). There has also been evidence to demonstrate that corridors increase patch population density (Haddad and Baum 1999), interbreeding among patches (Mech and Hallett 2001), and inter-patch movement (Haddad 1999). In each of these cases movement in corridors was inferred from patterns of population redistribution which makes it difficult to identify the variety of factors that influence corridor use (Simberloff and Cox 1987, Simberloff et al. 1992, Andreassen et al. 1996). To accurately assess

whether or not corridors provide functional connectivity between isolated patches, more direct measures of corridor use, such as the precise trajectories of moving animals while they are traveling to find and use corridors, should be employed (Turchin 1991, Tischendorf and Wissel 1997, Haddad 1999). Examination of these specific movement patterns may reveal the mechanisms by which animals find and select particular corridor configurations. Corridor use may change with species-specific perceptions of landscape elements (e.g. Zollner & Lima 1997, Haddad 1999). Species-specific differences in the perception of and response to corridors may stem logically from differences in a large array of natural history characteristics (Ims 1995), ranging from body size to activity pattern and habitat selection.

In addition to variation in corridor efficacy as a function of species attributes, corridor function, and also necessity, may change predictably with landscape context. In developed nations roads networks have increase substantially in the last 50 years, fragmenting most terrestrial ecosystems and greatly restricting animal movement (Forman 1998). Roads can act as severe impediments to movement, potentially causing genetic differentiation among fragmented populations (Aars & Ims 1999). The Trans-Canada Highway (TCH) in Banff National Park appears to be a severe barrier that clearly interferes with the movement of a variety of large mammal species across the sensitive montane habitat of the Bow River Valley (Page et al. 1996). To facilitate movement across the TCH crossing structures, two overpasses and several underpasses of various sizes, have been constructed which, together with drainage culverts, function as movement corridors for a wide variety of animals (Clevenger & Waltho 2000, Clevenger et al. 2001, Gloyne & Clevenger 2001). These crossing structures provide an unusual

opportunity for replicated, experimental study of some of the characteristics of corridors that may generally facilitate animal movement through fragmented landscapes.

Basic questions concerning the effects on corridor efficacy of species natural history, landscape context, and characteristics of the corridors themselves can be studied in Banff with relevance to animals contending with fragmented habitats elsewhere. However, they are difficult to address with many of the rare and wide-ranging animals that have been studied in natural corridor-containing landscapes to date (Beier & Noss 1998). Instead, I examined these issues using three species of microtine rodents (meadow voles [*Microtus pennsylvanicus*], deer mice [*Peromyscus maniculatus*], and red-backed voles [*Clethrionomys gapperi*]) for which some responses may be generalized to other species. Individuals of all three species were translocated (*sensu* Crist et al. 1992, With 1994, Zollner and Lima 1999) across the TCH adjacent to different wildlife crossing structures such that animals could plausibly return to their capture locations using the crossing structures as corridors. In conjunction with these translocation experiments, I chose to examine the effects on return success of three kinds of corridor characteristics; corridor size, vegetative cover at corridor entrances, and the distance from corridors at which animals were released. Additional variation in corridor efficacy could be expected from differences in natural history characteristics of the three target species (Ims 1995). This variation includes differences in preferred habitat (open grasslands for meadow voles, forested habitats for red-backed voles, and a mix of the two for deer mice), diel activity patterns (meadow voles are primarily diurnal whereas the other two species are active mainly at night), and home range size.

There are several reasons that I chose the guild of species and corridor characteristics named above. Size is one corridor characteristic that has been assumed to be highly linked to corridor efficacy for both vegetated corridors (e.g. Bennett et al. 1994, Andreassen et al. 1996) and wildlife crossing structures (Yanes et al. 1995, Rodriguez et al. 1996, Clevenger et al. 2001). Previous studies have suggested that larger corridors tend to be more efficient conduits for movement than smaller corridors (Simberloff et al. 1992), but there has been almost no comparative empirical work to support this assertion (Beier & Noss 1998). Overhead cover is a second characteristic that can influence the use of crossing structures (Hunt et al. 1987, Yanes et al. 1995, Clevenger et al. 2001), perhaps providing a relatively inexpensive way to increase corridor efficacy. Distance that animals have to travel to use a corridor is a final characteristic that may influence their efficacy. If frequent exchange of individuals through a corridor is desirable, then it may be important to know how far animals will travel to use these features. Responses to corridors and to variation in all three of these corridor characteristics may be expected to change with natural history characteristics. My target species incorporate three ubiquitous sources of variation with their differences in habitat preference, activity pattern, and home range sizes. In addition to these advantages, mice and voles are ideal subjects for experimental manipulations (i.e. using an Experimental Model System approach *sensu* Wiens et al. 1993; see also Ims and Stenseth 1989, Matter and Mannan 1989, With et al. 1999) that are designed to examine basic biological mechanisms.

Extrapolating the principals obtained from small-scale studies that are possible with Microtine rodents to larger scale patterns and processes requires a homogeneity of scale effects. Fractal analysis (Dicke and Burrough 1988, Wiens 1989, Sugihara and May

1990, Wiens et al. 1995) is sometimes used to generalize movement effects across spatial scales (e.g. Crist et al. 1992, Ims et al. 1992) by comparing path tortuosity (the degree to which a path twists) with scale-independent metrics. Although there is some question as to whether fractal analysis represents a truly scale-independent metric of movement (Turchin 1996), fractals have been used to assess differences in movement patterns for different species and across a range of spatial scales in a scale-independent manner (With 1994, Nams 1996). I examined the effect of corridor size on crossing structure use, the effect of different amounts of cover on crossing structure use, and the distance animals will travel to use a crossing structure.

Methods

Field data were collected from 1 July to 15 October 2000 in the Bow River Valley along the Trans-Canada Highway (TCH) in Banff National Park, Alberta, Canada. The TCH in Banff extends along the bottom of the Bow valley and is a major transportation corridor that carries as many as 5 million people through the park per year (Clevenger & Waltho 2000). Over half of the length of the TCH within the park is four lanes, bordered on both sides by a 2.4 m high wildlife exclusion fence that is a very effective movement barrier to large mammals. To mitigate this barrier effect, the park has constructed 22 wildlife underpasses and 2 overpasses (Clevenger & Waltho 2000). Meadow voles, red-backed voles and deer mice were captured using Longworth live-traps baited with sunflower seeds and individuals were permanently marked using numbered metal ear tags (National Band and Tag Company, Monel™ #1). The sex of each captured animal was then determined via examination of ano-genital distance. Individuals were also inspected to

ascertain their reproductive condition and weighed with a Pesola™ spring scale to determine age classes (adult or juvenile).

Translocations were conducted to standardize the motivation that individuals would have to return across different crossing structure types in the course of returning to their home territories. This method involved capturing individuals three times within 50 m of wildlife crossing structure entrances to establish their residency and then moving them across the TCH to the desired release points in areas adjacent to crossing structures. These translocations were used to determine the elements that promote crossing structure use for mice and voles with a focus on the effect of structure type on crossing structure use (n = 36), the effect of different cover amounts in crossing structure use (n = 39), and the distance animals will travel to use a crossing structure (n = 91).

To assess preferences in crossing structure type, individuals were translocated directly across two wildlife overpasses with recent vegetative landscaping, nine 3 m-diameter wildlife underpasses with no vegetative cover inside or at the entrances, and nine 0.3 m-diameter metal drainage culverts. To determine the role of ground cover in improving the function of crossing structures, I translocated individuals across two wildlife overpasses (n = 13) and nine 3 m-diameter wildlife underpasses (n = 26). Prior to all translocations, the amount of the cover (heavy, medium, or none) was varied at the entrances to crossing structures using freshly cut spruce boughs to represent natural cover. In the heavy, medium, and no cover treatments approximately 100%, 50% and 0%, respectively, of the area within 2 m of the entrances to the wildlife crossing structures had spruce boughs applied. To quantify the distance individuals would travel to use crossing structures I captured individuals adjacent to the TCH and translocated

them directly across the road to similar habitat adjacent to 3 m-diameter wildlife underpasses. Animals were captured and released at distances of 20 m, 40 m, and 60 m from underpasses (Fig. 3-1).

Prior to their release, all animals were marked with a small quantity of fluorescent powder (Radiant™ fluorescent pigment), which later fell off as animals moved along the ground, permitting the fine-scale monitoring of movement paths (Lemen & Freeman 1985, Mikesic & Drickamer 1992). Movement responses were quantified as the return success and path characteristics of individuals as they encountered crossing structures. I monitored traps at each individual's original capture location for 4 days following its translocation to determine the proportion of translocated animals that returned successfully. Each animal that failed to return within four days was captured at or near it's release location and returned manually. Because no experimental subjects disappeared or were killed on the highway (N = 166), I was able categorize every translocated animal as having either succeeded (n = 90) or failed (n = 76) to return.

Mice and voles were released 2 m from the entrances to crossing structures at the beginning of their active periods; early morning for the diurnal meadow voles and early evening for the nocturnal deer mice and red-backed voles. The subsequent path of each translocated individual was followed the next evening with a hand-held ultraviolet light, which caused the pigment in the dye to fluoresce, revealing a bright trail representing the animal's precise trajectory. Wire pin flags were placed along the trails at each turn where the compass bearing differed by at least 20 degrees from the previous bearing (derived after Turchin 1998). By subtracting the compass bearing of each step (the straight-line

distance between sequential turns) from the bearing of the subsequent step, I converted the bearings to turning angles for subsequent analysis.

To calculate the squared net displacement of the path, (the square of the total distance that an animal had traveled from the release point to the end of the path) in a given habitat, step lengths and turning angles were converted into XY coordinates. I employed net displacement squared, because it is expected to increase linearly with time (Turchin 1998) whereas measures of simple net displacement tend to be biased in both duration and length by longer paths (Wiens et al. 1993). Dividing the total path length by the net displacement squared yielded an estimate of the overall path tortuosity, which I considered to be an estimate of the costs associated with a particular movement pattern.

I analyzed the binary dependant variable, return success, with logistic regression using a model-building strategy described by Hosmer and Lemeshow (1989). To allow for the inclusion of biologically important variables in the model, univariate tests were conducted with an alpha level set liberally at 0.25 to identify significant main effects from all candidate variables. Species type (deer mice, meadow voles, and red-backed voles), translocation type (the crossing structure preference experiment variables were: overpasses, 3m-diameter underpasses, 0.3m-diameter culverts; the cover experiment variables were: heavy, medium, and no cover; the distance to crossing structure experiment variables were: 20m, 40m and 60m), translocation distance (the distance animals were moved across the TCH between the original capture location and release point), and sex were identified *a priori* as potential candidate variables. All variables that the univariate tests identified as significant were fitted into a combined model, and of those variables, any identified as significant using Wald statistics were fit in a reduced

model. To assess the effect of variables that were removed, but confounded with the remaining variables, changes in the *beta* coefficients of the remaining variables with and without the non-significant variables were examined. The linear assumptions of the continuous variables were tested using a likelihood ratio test comparing a model containing only the linear term to a model with the addition of the quadratic term. A list of potentially biologically important interaction terms was prepared and entered, one term at a time, into the reduced main-effects model. The significance of these interaction terms was assessed with Wald statistics and verified with a likelihood ratio test examining changes in deviance between the models with and without the interaction term. Finally, a reduced model with the significant main effects and interaction terms was constructed and it's fit to the data assessed using the Nagelkerke's r^2, which provides an approximate measure of the strength of association between the dependent and independent variables. The Hosmer and Lemeshow test statistic was also used to assess the fit of models produced by the logistic regression model (1989). Hosmer and Lemeshow probability values approaching 1.0 indicate that the candidate model fits the data quite well. The qualitative results of the analyses were unchanged when backward stepwise logistic regression was performed in addition to the model building procedure described above.

I used multi-variate ANOVAs to analyze scale-dependant path elements such as tortuosity and fractal dimension. This was only done for two experiments: the role of cover amount in crossing structure use and the distance animals will travel to find a crossing structure, because detailed path data could not be collected in the small crossing structures that were used in the crossing structure preference component. Species type

(deer mice, meadow voles, and red-backed voles), translocation type (the crossing structure preference experiment variables were: overpasses 3m-diameter underpasses, 0.3m-diameter culverts; the cover experiment variables were: heavy, medium, and no cover; the distance to crossing structure experiment variables were: 20m, 40m and 60m), translocation distance (the distance animals were moved across the TCH between the original capture location and release point), and sex were identified *a priori* as potential candidate variables. Two-way interaction terms were entered into the models (species by translocation type, species by sex, and sex by translocation type). Posthoc analyses via Tukey's honestly significant difference (HSD) tests were used to determine the significance of pairwise comparisons among several means (Zar 1996). I assessed the model's fit to the data using the adjusted r^2. Tortuosity measures did not meet assumptions of normality, so log transformations were performed to normalize the data.

Fractal geometry was used as a scale-independent measure of movement responses. For further discussion of how fractal dimensions can be calculated and used see Chapter 2 Methods.

Results

The number of translocated animals that successfully returned to their original capture locations in the crossing structure preference experiment was affected by crossing structure type (Logistic Regression (LR): x^2 =13.5, df = 2, P = 0.004) and species (LR: x^2 = 8.9, df = 2, P = 0.011), but not by sex (LR: x^2 = 0.56, df = 1, P = 0.45) or translocation distance (LR: x^2 = 0.98, df = 1, P = 0.32). The overall model (LR: x^2 = 30.67, df = 8, $P <$ 0.001) provided a good fit to the data (*Nagelkerke* r^2 = 0.56, Hosmer & Lemeshow (H&L) test: x^2 = 3.8, df = 8, P = 0.87, % correctly classified in 0 and 1 categories: 68 and 86

respectively). All species were more successful returning through 0.3m-diameter culverts than through 3m-diameter underpasses, and least successful returning across overpasses. Deer mice had higher return success than the other two species through all crossing structures, while meadow voles exhibited the lowest return success across all structures or were unable to return altogether (Fig. 3-2).

When investigating the role of vegetative cover in crossing structure attraction, I found that return success was affected by the amount of cover provided (Logistic Regression (LR): x^2 =6.88, df = 2, P = 0.032) and species (LR: x^2 = 7.15, df = 2, P = 0.028), but not by sex (LR: x^2 = 0.033, df = 1, P = 0.86) or translocation distance (LR: x^2 = 0.005, df = 1, P = 0.94). The overall model (LR: x^2 = 15.5, df = 4, P = 0.004) provided a good fit to the data (*Nagelkerke* r^2 = 0.50, Hosmer & Lemeshow (H&L) test: x^2 = 1.1, df = 7, P = 0.88, % correctly classified in 0 and 1 categories: 75 and 79 respectively). Individuals were much more successful returning through crossing structures with heavy cover provided at the entrances than through structures with medium or no cover provided. Meadow voles experienced much lower return success through all crossing structures than did either deer mice or red-backed voles (Fig. 3-3).

Path tortuosity changed when different amounts of cover were provided (ANOVA: $F_{2,39}$ = 7.49, P = 0.003, *adjusted* r^2 = 0.59, Fig. 3-4a). Similar to the pattern observed for return success, individuals exhibited more tortuous movement paths when heavy cover was provided than in either the medium (Tukey's HSD: mean diff = 0.22, P = 0.031) or no cover treatments (Tukey's HSD: mean diff = 0.68, P < 0.001). Paths were also more tortuous in the medium cover treatment than when no cover was present (Tukey's HSD: mean diff = 0.45, P < 0.001). There were further significant tortuosity differences among

species (ANOVA: $F_{2,39} = 11.29$, $P < 0.001$). Deer mice moved in a significantly less tortuous manner when moving through all cover amounts than did red-backed voles (Tukey's HSD: mean diff = -0.29, $P = 0.004$) or meadow voles (Tukey's HSD: mean diff = -0.79, $P < 0.001$). Red-backed voles, in turn, exhibited less tortuous paths than meadow voles (Tukey's HSD: mean diff = -0.50, $P < 0.001$). There were no differences in the tortuosity of paths as a function of sex (ANOVA: $F_{1,39} = 0.46$, $P = 0.50$). A significant interaction between cover amount and species in the degree of tortuosity exhibited for each path revealed that meadow voles showed disproportionately high tortuosity under heavy cover, a habitat least similar to their preferred open meadow, relative to the medium and no cover treatments (ANOVA: $F_{4,39} = 7.09$, $P = 0.001$). There were no significant interactions between sex and cover amount (ANOVA: $F_{2,39} = 0.061$, $P = 0.94$) or species and sex (ANOVA: $F_{2,39} = 0.32$, $P = 0.73$).

Fractal geometry was used as a complementary, but scale-independent, measure of movement responses to different cover amounts. Fractal dimensions of individual paths differed significantly among the different cover amounts (ANOVA: $F_{2,39} = 156$, $P < 0.001$, *adjusted* $r^2 = 0.82$, Fig. 3-4b). As with the scale-dependent tortuosity measurement, mice and voles had significantly higher fractal values, indicating that they moved in more complex lines, in the heavy cover treatment than in the medium (Tukey's HSD: mean diff = 0.11, $P < 0.001$) or no cover treatments (Tukey's HSD: mean diff = 0.16, $P < 0.001$). Also like the pattern observed for path tortuosity, individuals moving through medium cover had significantly higher fractal dimensions than when no cover was present (Tukey's HSD: mean diff = -0.052, $P < 0.001$) and these differences were consistent among species. Although the qualitative response to different cover amounts

was similar among species, absolute fractal dimensions differed (ANOVA: $F_{2,39} = 28.8$, $P < 0.001$). Again, like the pattern observed for return success and tortuosity, deer mice paths had lower fractal D estimates than either red-backed voles (Tukey's HSD: mean diff = -0.064, $P < 0.001$) or meadow voles (Tukey's HSD: mean diff = -0.087, $P < 0.001$) and red-backed vole paths had marginally lower fractal values than meadow voles (Tukey's HSD: mean diff = -0.023, $P = 0.053$). Sex had no effect on the fractal values of translocated animals (ANOVA: $F_{1,39} = 3.12$, $P = 0.099$). Among the three interaction terms I investigated, only cover amount by species was significant, and indicated proportionately more complex paths displayed by meadow voles in medium cover and deer mice in heavy cover (ANOVA: $F_{4,39} = 5.25$, $P = 0.004$).

The return success of individuals using crossing structures was affected by the distance at which they were released from crossing structures (Logistic Regression (LR): $x^2 = 9.16$, df = 2, $P = 0.010$) and species (LR: $x^2 = 23.8$, df = 2, $P < 0.001$), but not by sex (LR: $x^2 = 1.26$, df = 1, $P = 0.262$) or translocation distance (LR: $x^2 = 0.57$, df = 1, $P = 0.449$). The overall model (LR: $x^2 = 38.2$, df = 4, $P < 0.001$) provided a good fit to the data (*Nagelkerke* $r^2 = 0.53$, Hosmer & Lemeshow (H&L) test: $x^2 = 1.69$, df = 6, $P = 0.95$, % correctly classified in 0 and 1 categories: 81 and 80 respectively). Individuals were less successful returning to crossing structures as the distance from an animal's home territory increased. It appeared that this effect was driven mainly by the very low return success exhibited by animals translocated 60 m from crossing structures because there was no significant difference in return success between animals translocated 20 m and 40 m from crossing structures. Meadow voles had the lowest return success across all distances, while deer mice tended to return most often (Fig. 3-5).

To corroborate my return success results, I once again compared the tortuosity of paths using ANOVA. The distance that animals had to travel to crossing structures influenced path tortuosity (ANOVA: $F_{2,91} = 18.1$, $P < 0.001$, *adjusted* $r^2 = 0.68$, Fig. 3-6a). Animals translocated 60 m from crossing structures moved in a more tortuous manner than those that only had to move 40 m (Tukey's HSD: mean diff = 0.44, $P < 0.001$) or 20m (Tukey's HSD: mean diff = 0.59, $P < 0.001$) to find crossing structures. As for return success, no difference in tortuosity existed between paths at 20 m and 40 m (Tukey's HSD: mean diff = -0.15, $P = 0.34$). There were also significant tortuosity differences among species (ANOVA: $F_{2,91} = 7.18$, $P = 0.017$). Meadow voles moved in a much more tortuous manner when attempting to return to crossing structures than did red-backed voles (Tukey's HSD: mean diff = 0.87, $P < 0.001$) or deer mice (Tukey's HSD: mean diff = 1.34, $P < 0.001$). Deer mice, which are able to use a variety of habitats, exhibited less tortuous paths than red-backed voles that use primarily forest habitat (Tukey's HSD: mean diff = -0.47, $P < 0.001$). Sex had no impact on path tortuosity (ANOVA: $F_{1,91} = 0.50$, $P = 0.48$). A significant interaction between the distance traveled to crossing structures and species was driven mainly by disproportionately higher than expected tortuosity by meadow voles at 20m and 60m (ANOVA: $F_{4,91} = 4.74$, $P = 0.003$). There were no significant interactions between sex and cover amount (ANOVA: $F_{2,91} = 1.18$, $P = 0.33$) or species and sex (ANOVA: $F_{2,91} = 0.79$, $P = 0.46$).

As before, I calculated scale-independent fractal dimensions and compared them with an ANOVA to determine if the observed movement responses were due to life-history characteristics or to differences in spatial scale. Unlike the pattern observed in path tortuosity, fractal dimensions of individual paths did not differ significantly based on the

distance from crossing structures (ANOVA: $F_{2,91} = 0.79$, $P = 0.46$, *adjusted* $r^2 = 0.21$, Fig. 3-6b), which suggests that the apparent tortuosity difference above may be an artifact of larger scale. Animals at 60 m away from crossing structures had similar fractal values to paths at 40 m (Tukey's HSD: mean diff = 0.037, $P = 0.43$) or at 20 m (Tukey's HSD: mean diff = 0.021, $P = 0.75$), indicating that they interacted with the landscape with comparable complexity. Like the pattern observed for path tortuosity, there were no significant differences between the fractal dimensions of individuals traveling from 20 m and 40 m away from crossing structures (Tukey's HSD: mean diff = 0.016, $P = 0.86$). Fractal dimensions did not differ among species (ANOVA: $F_{2,91} = 1.66$, $P = 0.20$). Deer mice paths had fractal D estimates that were comparable with both red-backed voles (Tukey's HSD: mean diff = 0.049, $P = 0.19$) and meadow voles (Tukey's HSD: mean diff = -0.050, $P = 0.26$). Red-backed vole paths had similar fractal values to meadow voles (Tukey's HSD: mean diff = 0.031, $P = 0.42$). Sex had no effect on the fractal values of translocated animals (ANOVA: $F_{1,91} = 1.5$, $P = 0.22$). None of the three interaction terms I investigated was significant.

Discussion

I investigated the effect of different types of wildlife crossing structures, small culverts, large underpasses as well as overpasses, on the propensity of translocated deer mice, meadow voles, and red-backed voles to successfully return to their original capture location. Microtines were more successful returning through 0.3m-diameter drainage culverts than through 3m-diameter underpasses, and least successful returning across overpasses. Previous studies have demonstrated that the dimensions of crossing structures are an important attribute determining corridor use for vertebrates, but animals

generally favour wider structures (Reed et al. 1975, Hunt et al. 1987, Harrison 1992, Rosell et al. 1997). In general, movements through narrow corridors are expected to be more risky than movement through wider corridors, presumably due to the higher influence of edge effects such as predation (Simberloff & Cox 1987, Noss 1987, Patton 1994, Andreassen et al. 1996). However, small animals may perceive predation risk in crossing structures in exactly the opposite direction (Hunt et al. 1987, Rodriguez et al. 1996), leading to lower crossing successes there. For them, the presence of denser and more proximate overhead cover, which these animals generally prefer (Diffendorfer et al. 1995), may have made the smaller structures seem safer. The high return success of nocturnal deer mice through all crossing structures was potentially linked to lower traffic volume at night, which has been found to affect crossing structure use in a variety of small and medium sized animals in the same study area (Clevenger & Waltho 2000). The preference for small drainage culverts exhibited by small mammals in this study supports the suggestion that the movement of these animals across the TCH may be substantially enhanced by existing below-road passages such as drainage culverts (Clevenger & Waltho 2000, Clevenger et al. 2001).

The return success results across different sizes of crossing structures may have been artificially high due to previous use of the crossing structures by some of the translocated animals. Thus, these animals may have been able to return more successfully because they were in the presence of familiar landscape cues. However, small mammals tend to align their territories to physical features such as roads, which results in the organization of social spacing along such features (Barnett et al. 1978, Stamps et al. 1987) rather than across roads. Therefore it is unlikely that any translocated small mammals were released

in familiar territory (i.e. their home-range) on the other side of crossing structures (Burnett 1992). Crossing structure use may also have been increased by conspecific cues left behind by individuals that previously traveled through the crossing structures (Smith & Peacock 1990, Reed & Dobson 1993), although any such effect may been negligible (Andreassen et al. 1996). The effect of such conspecific attraction was probably minimal because the linear arrangement of small mammal home-ranges along the TCH would reduce the use of the underpasses and overpasses.

Consistent with crossing structure dimension as an influence on small mammal passage, the amount of cover at underpass and overpass entrances also affected the return success of translocated animals. Other studies have also found that tree and shrub cover at corridor entrances increased their efficacy (Rodriguez et al.1996, Rosell et al. 1997). Meadow voles exhibited much lower return success under all cover amounts and were unable to return at all when no cover was provided, possibly due to their diurnal activity and the corresponding high traffic volumes along the TCH. During the daylight hours, traffic volumes on the TCH are significantly higher than those occurring at night, varying from peak values of 20 000 vehicles during the day to less than 5 000 vehicles at night (Clevenger & Waltho 2000). Consequently, meadow voles encountered elevated vehicle noise, vibration, and movement when attempting to return through crossing structures compared to the two nocturnal species. An alternative explanation for the reluctance of meadow voles to use crossing structures may be their relative lack of mobility compared to deer mice (Banfield 1981), which may have reduced their ability to perceive the patchiness of the environment (Carpenter 1987).

All mice and voles were more successful returning through crossing structures with heavy cover at the entrances than through structures with medium or no cover provided. Thus my results indicate that the effectiveness of crossing structures may be improved by adding overhead cover, including artificial cover like my spruce boughs, to confer greater freedom of movement and provide vulnerable small mammals with protection from predation (Hunt et al. 1987, Rosell et al. 1997). However individual return success alone is not adequate as a direct measure of crossing structure use, so I also measured the precise trajectories of moving animals (Turchin 1991, Tischendorf and Wissel 1997, Haddad 1999).

Path tortuosity and fractal dimensions were measured to examine the mechanisms potentially responsible for differences in mice and vole return success, as more complex, paths could result in lower return success through wildlife crossing structures (Stamps 1987). Deer mice exhibited lower path tortuosity when moving through all cover amounts than did red-backed voles or meadow voles, which led, in turn, to substantially higher return success. Meadow voles exhibited much more tortuous paths under heavy cover, presumably because they had limited ability to perceive the most direct route through the heavy overhead cover. However contrary to the predicted direct proportional association between return success and tortuosity, all individuals exhibited more tortuous movement paths when heavy cover was provided than in either the medium or no cover treatments. Thus, a highly complex path does not necessarily diminish return success as predicted, particularly in the context of animals encountering heavy overhead cover and potentially being unable perceive a direct route to their destination. In addition, animals may have attempted to move more quickly and directly when no overhead cover was

present to avoid higher perceived predation risks (Stapp & Van Horne 1997). Although heavy cover allowed for the highest return success, my results also indicate that providing any amount of cover substantially improves crossing structure use for all species.

Fractal analysis can be used to allow these movement effects to be more easily generalized across spatial scales (e.g. Crist et al. 1992, Ims et al. 1992) by comparing path tortuosity with scale-independent metrics. The differences observed in path tortuosity that were attributed to species and cover amount may in fact be due to life history differences such as home-range or territory size because tortuosity is a scale-dependent metric. Species with larger territories such as deer mice (approx. 1.2 ha) may operate on a larger spatial scale than species with smaller territories such as red-backed voles (approx. 0.7 ha) and meadow voles (approx. 0.1 ha). When controlled for scale, animals under heavy cover generally interacted with the landscape in a more complex manner, while meadow voles had much more complex movement paths than did deer mice or red-backed voles across all cover amounts. These results are qualitatively consistent with the tortuosity and return success values described above. Thus, it appears that the movement responses of deer mice, meadow voles, and red-backed voles to different amounts of cover are not influenced by spatial scale, or at least by the range of scales encompassed by the territory sizes of these species.

The amount of cover present at underpass and overpass entrances and the dimensions of crossing structures both appear to influence the efficacy of crossing structures. However, this information about the elements that promote corridor use could be more valuable to conservation planning in combination with knowledge about how far animals will travel to use corridors (Rosenberg and Noon 1997). The probability of animals using

a corridor depends to a large extent on the chance that an animal can find a given corridor (Simberloff et al. 1992, also see Walters et al. 1988). The ability of animals to return to crossing structures successfully was validated by the existence of similar patterns in path tortuosity at all three distances. Diurnal meadow voles that typically live in open habitat had the lowest return success and most tortuous paths across all distances, while deer mice, which are able to use a variety of habitats, tended to return most often while moving in relatively straight lines. All three species were less successful and moved more tortuously when returning to crossing structures as the distance from an animal's capture site increased, although this effect was driven mainly by very low return success for animals translocated 60 m from crossing structures. Indeed, return success and tortuosity did not differ significantly between animals translocated 20 m and 40 m from crossing structures. The decline in animal use of crossing structures as the distance to the structure increases may have important implications for the future placement of wildlife corridors in fragmented landscapes. Previous studies have made recommendations concerning corridor density on the landscape aimed at improving habitat connectivity without explicitly identifying how far animals will travel to use these corridors (e.g. Clevenger & Waltho 2000). My results indicate that if frequent use of crossing structures is desired for a particular target species, these structures may need to be constructed at distances commensurate with species-specific territory sizes to have a conservation impact.

As with the cover analysis, fractal dimensions were calculated for all distance analysis paths to determine if the differences observed in return success and path tortuosity that were attributed to species and distance were in fact due to differences in

territory size. Deer mice (home-range: 1.2 ha; Gunderson 1959) move on a larger spatial scale than species with smaller territories such as red-backed voles (home-range: 0.7 ha; Jones & Knox 1983) and meadow voles (home-range: 0.1 ha; Banfield 1981). I found that, when controlled for scale, animals at all three distances generally exhibited paths with almost identical complexity, perhaps indicating that territory size may be more important in determining how far animals will travel to use a crossing structure than species habitat preferences and activity patterns. Similarly, Bowman et al. (2002) concluded that the distance animals will disperse or travel following translocations was better predicted by home-range size than by body size. Both of these results suggest that the vagility of mammals, which can affect home-range size and dispersal distance (Bowman et al. 2002), should be taken into account when trying to determine the optimum travel distance between crossing structures for a given species.

In summary, it appears that crossing structure dimensions are important determinants of corridor use (Hunt et al. 1987, Rosell et al. 1997), where small mammals tend to use smaller crossing structures more than larger underpasses or overpasses. Therefore, as other studies have suggested, it appears that bigger is not necessarily better when it comes to corridor design for prey species and other small fauna (e.g. Andren & Angelstam 1988, Saunders & Hobbs 1991, Harrison 1992, Andreassen et al. 1996). Animals appear to select corridors that are scaled relative to their body size, perhaps because wide corridors represent livable habitat, particularly the edges (Andreassen 1996) where predation risk is elevated (Simberloff & Cox 1987, Harrison 1992, Patton 1994). Mice and voles relied heavily on overhead cover, presumably to lower the perceived risk of predation (Stapp & Van Horne 1997), when moving through crossing structures with various amounts of

cover at the entrances. Therefore, supplying overhead cover in the form of logs and brush piles at the entrances to large underpasses may encourage small mammals to cross and afford a relatively inexpensive way of improving their effectiveness. Small mammals appear to be reluctant to travel to crossing structures when the distance exceeds the animal's home-range size, perhaps because they are hesitant to cross the territory of a conspecific to reach a corridor (Burnett 1992, Andreassen et al. 1996). Essentially identical fractal dimensions in the distance component may indicate that territory size is more important than life-history characteristics or distance in determining how far animals will travel to use a crossing structure. The importance of territory size is indicated if, when spatial scale is controlled, movement patterns change compared to scale-dependent tortuosity values, as was the case it this instance. However, because the relatively limited range of territory sizes encompassed by these three species restricts the generality of any such assertion, future work should focus on testing the responses of animals that incorporate a greater range of territory sizes.

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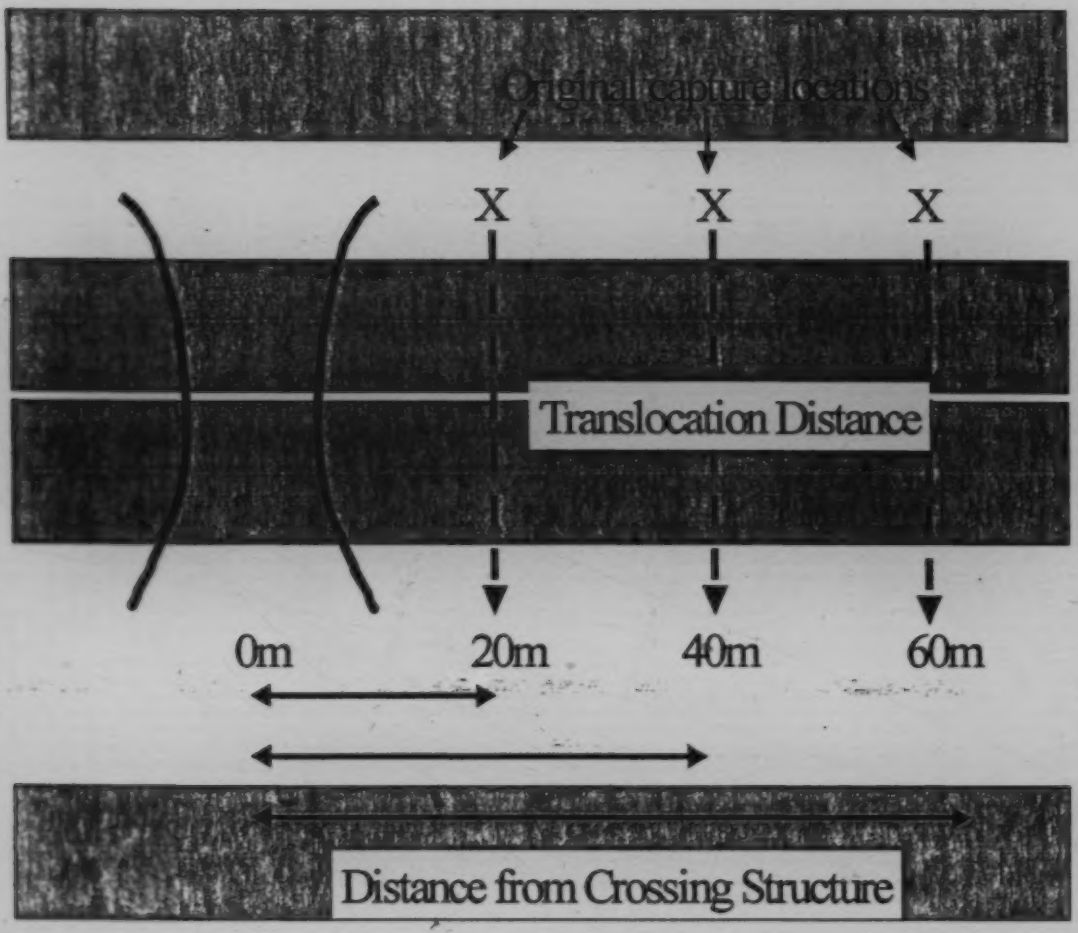

Figure 3-1: Schematic of translocations at distances of 20 m, 40 m, and 60 m from crossing structures showing original capture and release locations along the Trans-Canada Highway.

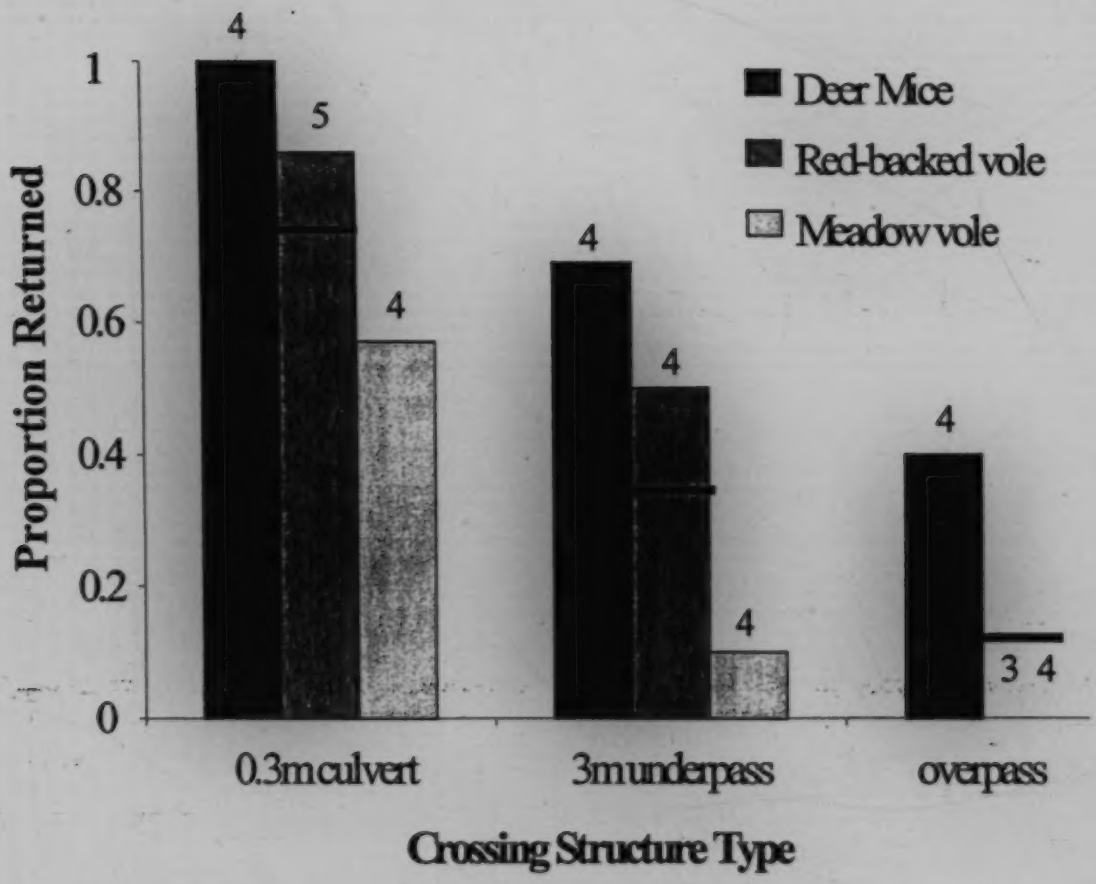

Figure 3-2: Proportion of deer mice, meadow voles, and red-backed voles that successfully returned following translocations across 0.3m-diameter underpasses, 3m-diameter underpasses, and overpasses. Black lines represent the adjusted means for each barrier type. Sample sizes (n) are above each bar.

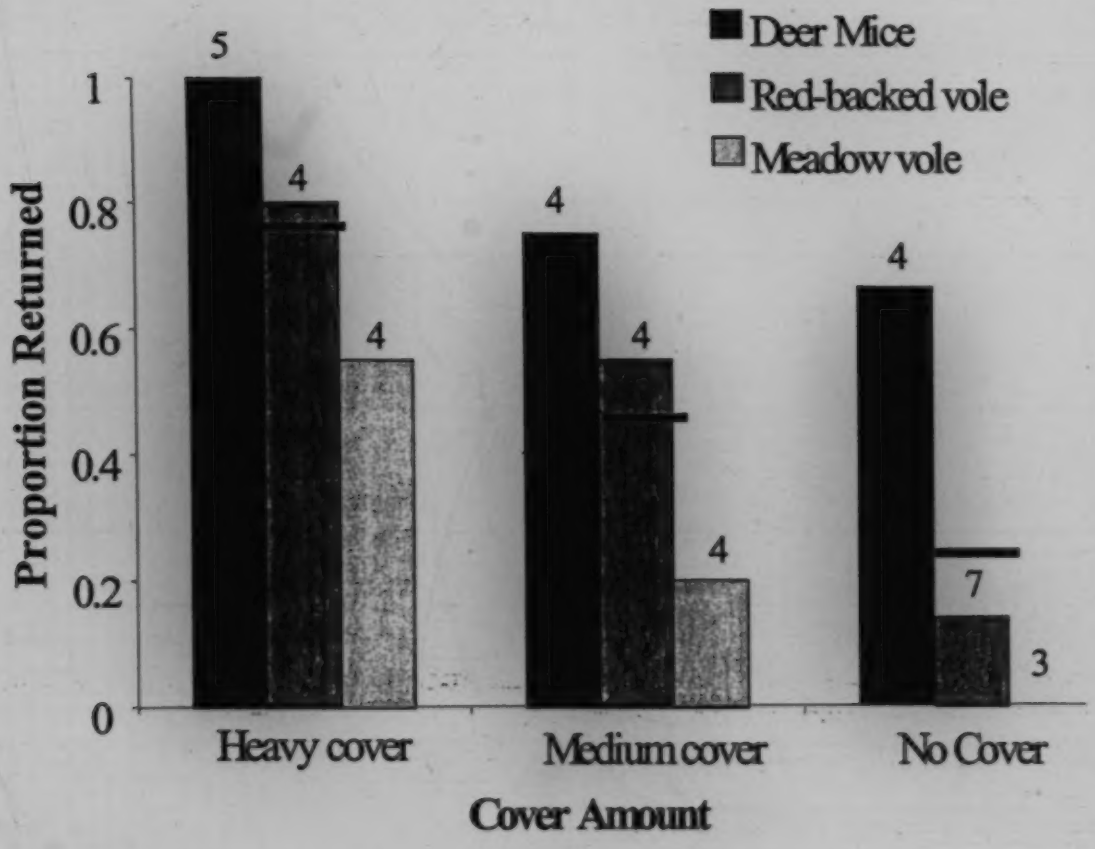

Figure 3-3: Proportion of deer mice, meadow voles, and red-backed voles that successfully returned following translocations under heavy, medium, and no cover treatments. Black lines represent the adjusted means for each barrier type. Sample sizes (n) are above each bar.

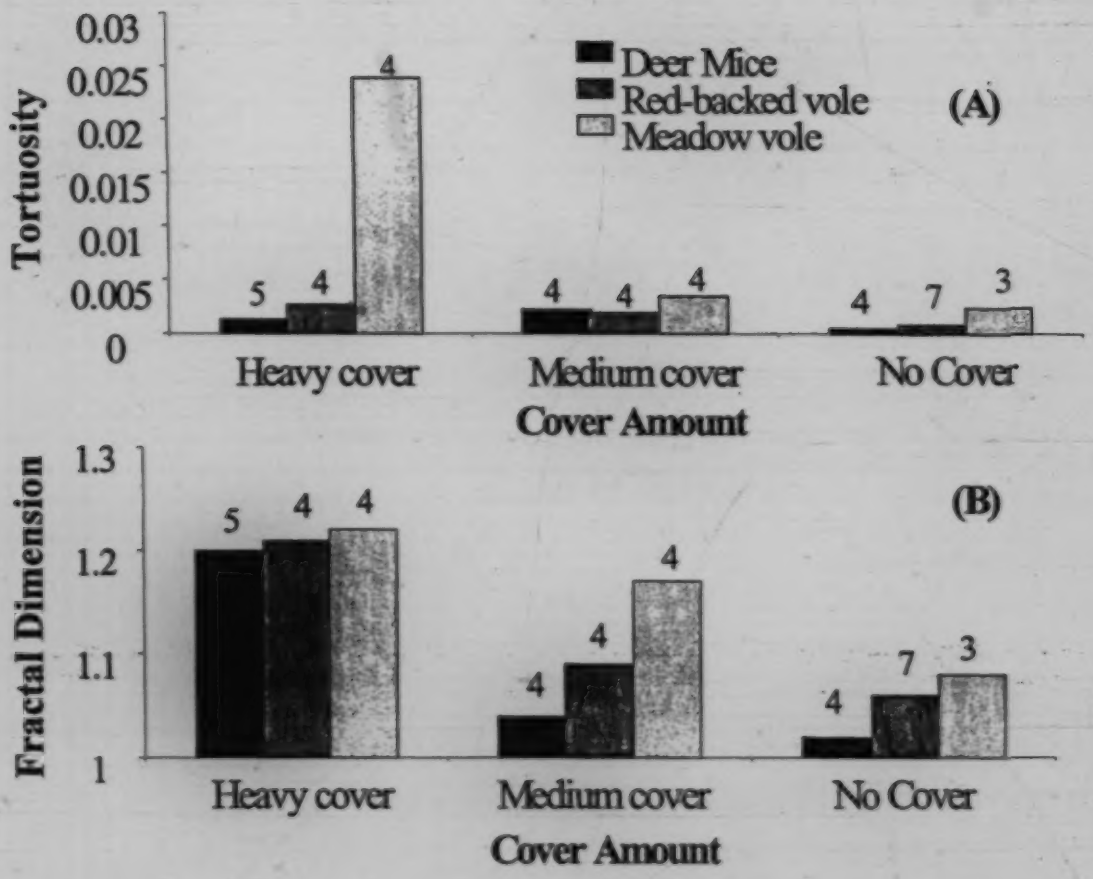

Figure 3-4: (a) Tortuosity values (total path length divided by net displacement squared) and (b) fractal dimensions of translocated deer mice, meadow voles, and red-backed voles encountering heavy, medium and no cover treatments. Sample sizes (n) are above each bar.

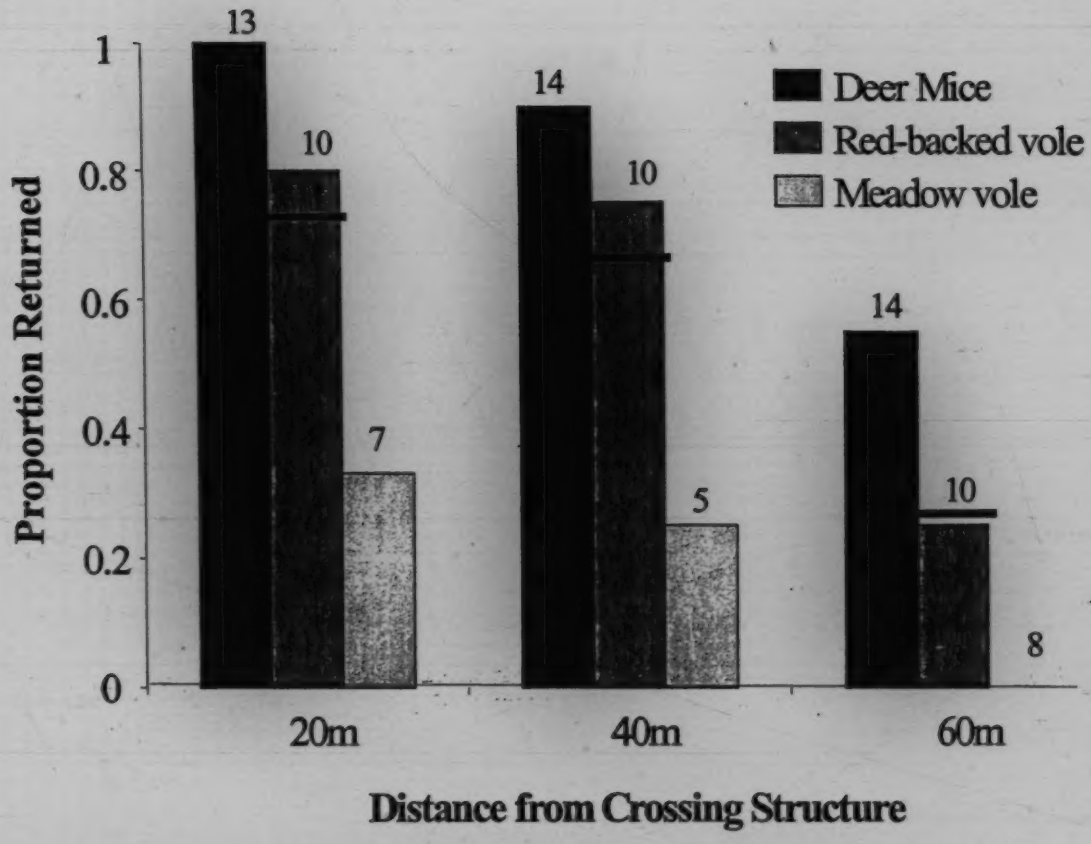

Figure 3-5: Proportion of deer mice, meadow voles, and red-backed voles that successfully returned following translocations at distances of 20 m, 40 m, and 60 m from crossing structures. Black lines represent the adjusted means for each barrier type. Sample sizes (n) are above each bar.

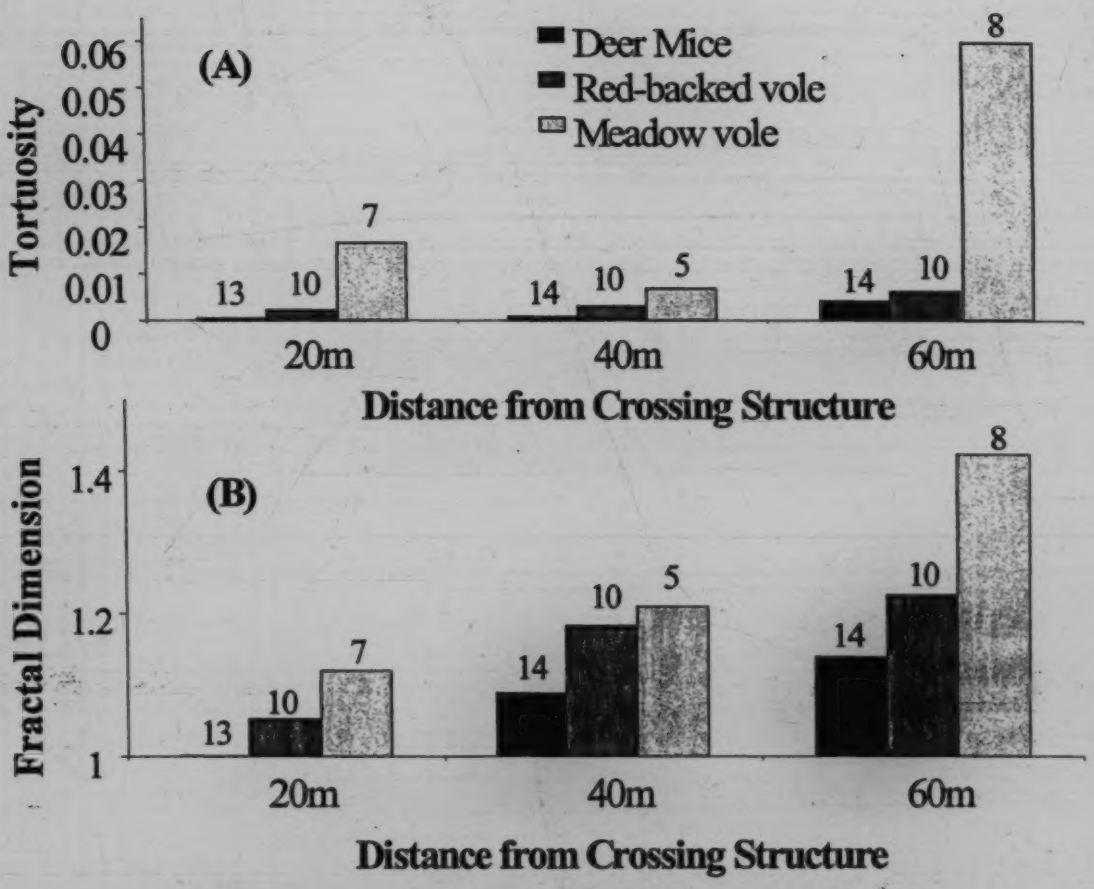

Figure 3-6: (a) Tortuosity values (total path length divided by net displacement squared) and (b) fractal dimensions of translocated deer mice, meadow voles, and red-backed voles returning from distances of 20 m, 40 m, and 60 m from crossing structures. Sample sizes (n) are above each bar.

Chapter 4 - General Discussion

Anthropogenic features, such as roads, in the midst of continuous habitat can act as absolute barriers to animal movement (Kozakiewicz 1993), or can filter animal movement by creating complex movement paths. To mitigate the effect of barriers on animal movement, corridors have been widely advocated in conservation strategies (Noss 1987, Saunders et al. 1991). I investigated how small mammals responded to barriers and corridors and whether movement responses varied with habitat preferences (e.g. Ingham and Samways 1996) and activity strategies. In Banff National Park the Trans-Canada Highway (TCH), along with the associated overpasses and underpasses, provided a standardized system to assess the responses of animals to barriers and corridors. I used three species of microtine rodents that prefer a range of habitats and diel activity and for which some responses may be generalized to other species. The sensitivity of animals to habitat fragmentation may depend to some extent on these species-specific, natural history characteristics (Ims 1995).

Animals encountering anthropogenic barriers may exhibit very different movement patterns than animals at natural barriers. Part of an animal's response to barriers is determined by return success across barriers, a simple quantitative metric of barrier permeability (Stamps et al. 1987). However, it may also be important to quantify movement responses as path complexity adjacent to the barrier and changes in movement patterns across spatial scales. In Chapter 2, I estimated the permeability of the TCH to movement relative to natural barriers and continuous habitat. Individuals crossing artificial barriers had lower return success and more complex path structures than individuals crossing natural barriers, indicating that artificial barriers are less permeable

to movement. However the road appears to cause only a slight barrier to movement because individuals were just 20% less likely to return across artificial barriers than in continuous habitat. I concluded that the TCH may act as a filter for small mammal movement across the Bow Valley rather than an absolute barrier preventing individuals from crossing the road (*sensu* Bennett 1992, Forman 1995). Meadow voles found artificial barriers to be much less permeable than any other species at any other barrier type, possibly due to their diurnal activity and subsequent exposure to high traffic volumes along the TCH (Clevenger & Waltho 2000). I concluded that the movement responses of deer mice, meadow voles, and red-backed voles to barrier permeability are not influenced by spatial scale by determining that there were no significant differences in path fractal values. Therefore I can be reasonably confident that the observed movement patterns of mice and voles are driven by the physical characteristics of barriers or species life-history, rather than by the spatial scale at which a particular species moves.

Many conservation plans have advocated the construction or conservation of habitat corridors to facilitate the movement of a variety of animals through fragmented landscapes (Bennett 1990, Merriam 1991, Simberloff et al. 1992). In Chapter 3, I chose to examine the effects on return success of three kinds of corridor characteristics; corridor size, vegetative cover at corridor entrances, and the distance from corridors at which animals were released. Animals returned with higher success across smaller crossing structures presumably because these structures afforded more overhead cover, indicating that bigger is not necessarily better when it comes to corridor design (e.g. Andreassen et al. 1996). Adding vegetative overhead cover to crossing structure entrances further improved return success and animal movement perhaps because it provided small

mammals, which are a prey source for many species, with protection from predation (Hunt et al. 1987, Rosell et al. 1997). Finally, crossing structure efficacy declined as the distance from an animal's home territory increased, perhaps because translocated individuals were hesitant to cross the territory of a conspecific to reach a corridor (Andreassen et al. 1996). In addition, the effect of distance on crossing success was inversely proportional to species home range size, but not body size, suggesting that species with larger home ranges can travel farther to use corridors. Together, my results indicate that ideal corridor characteristics will often be determined by the life-history of a given species and that corridors need to be placed with a frequency commensurate with the spatial scale over which targeted species are able to move.

In this study I demonstrated that artificial barriers are somewhat less permeable to movement based on individual return success and path complexity metrics. These patterns in return success and path complexity may to be based, in part, on species-specific habitat preferences (Ims 1995) and the extent to which microtines rely on overhead cover to move (Hunt et al. 1987, Rosell et al. 1997). Indeed, perceptions of permeability may change movement in ways that lessen the likelihood an animal will succeed in crossing a given feature even before the animal enters the feature and is impeded by it (Buechner 1987). Animals appear to select corridors that are proportionate to their body size, perhaps because wide corridors represent livable habitat (Andreassen 1996) for these small mammals, particularly the edges where predation risk may be elevated (Simberloff & Cox 1987, Harrison 1992, Patton 1994). Log and brush piles at the entrances to structures may encourage small mammals to cross and afford a relatively inexpensive way of improving their effectiveness. My results also indicate that species-

specific territory size may be the best predictor of the distance animals will travel to find a crossing structure. However, the relatively limited range of territory sizes represented by the three species of mice and voles that I used restricts the generality of any such assertion. Thus, future work focusing on testing the responses of animals that incorporate a greater range of territory sizes may be profitable.

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